



PEARL

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

Briffa, Mark; Lane, Sarah M.

Published in:

Proceedings of the Royal Society B: Biological Sciences

DOI:

[10.1098/rspb.2017.1596](https://doi.org/10.1098/rspb.2017.1596)

Publication date:

2017

Link:

[Link to publication in PEARL](#)

Citation for published version (APA):

Briffa, M., & Lane, S. M. (2017). The role of skill in animal contests: a neglected component of fighting ability. *Proceedings of the Royal Society B: Biological Sciences*, 284(1863). <https://doi.org/10.1098/rspb.2017.1596>

All content in PEARL is protected by copyright law. Author manuscripts are made available in accordance with publisher policies. Wherever possible please cite the published version using the details provided on the item record or document. In the absence of an open licence (e.g. Creative Commons), permissions for further reuse of content should be sought from the publisher or author.

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

2

3 Mark Briffa and Sarah M Lane

4

5 School of Biological and Marine Science,

6 Plymouth University,

7 Drake Circus,

8 Plymouth PL3 8AA,

9 United Kingdom.

10

11 Correspondence:

12 mark.briffa@plymouth.ac.uk

13

14 Short title: Skill in fighting animals

15

16

17 This is a manuscript version of an article published in *Proceedings of the Royal Society:*

18 *Biological Sciences* **284** (1863): 20171596. The version of record can be found at

19 <https://dx.doi.org/10.1098%2Frspb.2017.1596>

20

21

22

23

24

25

26

27

28

29

30

31

32

33 **ABSTRACT**

34

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

50

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

52

53

54

55 **INTRODUCTION**

56

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

69

70 *What makes a good fighter?*

71 For animals, unequal access to food, shelter, territories and even social status and mates can
72 constrain survival and reproductive rates [4]. Thus, individuals are likely to come into severe
73 conflict, particularly with conspecifics that require exactly the same resources. When these
74 conflicts are concentrated upon the ownership of a single indivisible resource unit the result is
75 a discrete interaction called a contest [4]. In addition to a resource, contests are characterised
76 by a set of opponents (usually two individuals), the use of agonistic behaviour and an
77 outcome that produces winners and losers. The word *contest* is often used synonymously with
78 *fight*, whereas some authors prefer to reserve the latter term only for the most intense

79 examples of contests where sustained physical contact occurs and there is the possibility of
80 injury. In less intense contests, outcomes might be decided by the use of signals or by trials of
81 strength, as in pushing or wrestling matches. In this review we use *fight* to describe all of
82 these levels of contest behaviour because they all involve the use of *agonistic behaviour*. This
83 is defined as aggressive or defensive behaviour used when attempting to directly exclude
84 other individuals from access to a resource that is usually indivisible [5] (although see [6] for
85 an example where resource units can be shared if opponents are evenly matched).

86 Fights are usually characterised by asymmetries in fighting ability between the
87 opponents. Fighting ability, often termed Resource Holding Potential (or Resource Holding
88 Power, RHP [7]), represents the phenotypic variation that differentiates winners from losers.
89 If both opponents value the resource equally, the individual with greater RHP should prevail
90 [8]. Therefore, enhanced RHP should offer a selective advantage and it is not surprising that a
91 central question in the study of contests should thus be centred on understanding which traits
92 contribute to RHP: In other words, what makes a good fighter? The importance of this
93 question goes beyond the initial identification of RHP traits. Once these are known they can
94 be used along with data on contest duration [9,10] and escalation patterns [10,11] to test the
95 hypothesis that losers reach their decision to give up either by comparing their RHP to that of
96 the opponent [12] or simply when their own individual threshold of costs is crossed [13,14].
97 Studies of fighting typically focus either on differences in physical or physiological RHP
98 traits [15] or on uncorrelated asymmetries between opponents that are determined by the
99 specific context of the fight, such as resource value [16] or the effect of prior ownership of
100 the resource [17]. It seems obvious that larger individuals should be likely to defeat smaller
101 ones [18,19] but differences in size can be further broken down into differences in weapon
102 size [20,21] and strength [3,22]. Strength is an example of a performance capacity and overall
103 stamina has also been revealed as an important performance capacity that can increase the

104 chances of victory [23]. Stamina in turn is dependent on energy reserves, aerobic capacity
105 [24] and metabolic rate [25]. Thus, morphological and physiological traits seem
106 fundamentally important to the outcome of animal fights.

107

108 *The nature of fighting*

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

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

146

147 **VIGOROUS FIGHTING**

148 When studies of fighting move beyond the measurement of physical traits and outcomes to
149 include analysis of agonistic behaviour itself, the focus tends to be on vigour [18]. Vigour is
150 defined as the intensity and rate of performance of an agonistic behaviour [34] and can be

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

172 While it is possible to show that on average winners fight more vigorously, and are
173 more likely to escalate than losers, there is a difficulty in establishing a given individual's
174 actual capacity for vigorous fighting. This is because an individual's vigour will vary from
175 fight to fight, as a consequence of variation in resource value and the RHP (and agonistic

176 behaviour) of different opponents. Thus, individual performance capacities have to be
177 quantified independently of fighting by measuring traits such as locomotor endurance [23] or
178 the closing force of appendages [22]. Studies applying these approaches indicate that
179 agonistic behaviour is energetically challenging and that the ability to fight vigorously is
180 strongly correlated with endurance capacity.

181

182 **SKILFUL FIGHTING**

183 While vigour and the chance of winning can vary with a host of physiological parameters that
184 drive endurance [15], endurance and hence sustained vigour might also be influenced by how
185 efficiently the required motor patterns are executed. Efficient movement is one component of
186 skill, which in the context of sexual selection Byers et al. [1] distinguish from vigour as
187 follows: If *vigour* represents the rate and intensity of a challenging behaviour, *skill* represents
188 how well the challenging behaviour is performed. In the context of fighting (and perhaps
189 courtship as well), how well a behaviour is performed encompasses its efficiency, accuracy,
190 precision and appropriateness to the situation. While *efficiency* refers to the minimum amount
191 of movement (and hence energy expenditure) required to perform a behaviour effectively,
192 *accuracy* refers to the degree of congruence between the motor patterns required (i.e. the
193 patterns that will influence the behaviour of recipients) and what is actually performed. As
194 well as signals that are attuned to the psychology of receivers (sensu [38]), accuracy could
195 encompass the delivery of strikes if the opponent must be struck on a specific body part (e.g.
196 on the telson in fighting mantis shrimp [39]). In addition to accuracy, *precision* may also be
197 important if victory depends on the consistency of agonistic behaviour within a fight, for
198 example repeatedly striking the same area of the opponent within narrow parameters of
199 variation. *Appropriateness* refers to the choice of agonistic tactics used in cases where there

200 is a range of possible choices and where the optimum tactic can vary between and within
201 fights, typically showing a pattern of escalation towards more costly tactics as the fight
202 progresses [12]. This is analogous to the concept of ‘game intelligence’ in human sports [2].
203 Inefficient agonistic behaviour would lead to reduced endurance while inaccurate or
204 inappropriate agonistic behaviour will produce ineffectual fighting. Thus, although vigour
205 and skill may be functionally linked (for example if sustained vigour is dependent on efficient
206 movement [34]) it is nevertheless possible to distinguish between the two, if vigour describes
207 temporal parameters of agonistic behaviour (rates) and skill refers to the spatial parameters
208 [1] of efficiency, accuracy, precision and appropriateness (Table 1).

209

210

211

212 *Skill is underpinned by ability and technique*

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

219 In sports training an analogous distinction is drawn between the potential to perform
220 movements well and the level of realised skill that is actually displayed in a real competition.
221 *Technique* is defined as the capacity to perform specific movement patterns whereas skill is
222 defined as the capacity to use these movements effectively during a competition. In

223 association football for example, dribbling the ball past static obstacles would require a
224 particular set of techniques. But using these techniques to dribble the ball past a real player,
225 without being dispossessed, would be an example of skill. Here, the correct ball-dribbling
226 techniques must be rapidly chosen and adjusted to counter the tackles of the defending
227 player. Similarly, in combat sports such as judo, the movement patterns required to throw the
228 opponent can be practised in training on a partner who will not resist. But again using the
229 same techniques against a real opponent, who will resist being thrown, would be an example
230 of skill.

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

247

248 **VARIATION IN ABILITY, TECHNIQUE AND SKILL**

249 *Variation in ability*

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

263 Variation in the musculoskeletal, nervous and sensory systems that should drive
264 variation in ability can be separated into genetic and environmental components. The genes
265 controlling neurogenesis are highly conserved across animals [42] and development of key
266 structures such as the cerebellum in vertebrates is increasingly well understood [43]. In
267 contrast, there are few examples where a direct link between genes and specific behaviours
268 have been demonstrated (see [44] for a review). In a more general sense, the links between
269 genotype and behaviour, including examples of variation in abilities that underpin technique,
270 can be demonstrated using quantitative genetics. In the field cricket, *Gryllus integer*, males

271 emit a stridulated call to attract females. The proportion of calls with long bout durations,
272 which are preferred by females, is highly repeatable across males. Call duration is also
273 heritable, indicating that much of this variation in calling ability between males is under
274 genetic control [45]. As well as being influenced by genes the structures that underpin
275 variation in ability will also be subject to developmental plasticity. Compensatory growth, for
276 example, allows individuals that are subjected to a poor diet early in life to achieve large
277 body size, via a prolonged growth phase, if diet improves later on during development.
278 However, developmental plasticity can come at a cost, for example in the swordtail,
279 *Xiphophorus hellerii*, prolonged growth results in reduced swimming speed and fighting
280 ability [46]. Thus, variation in ability is likely to be driven by interactions between genes and
281 environment.

282

283

284 *Variation in technique – the roles of development and experience*

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

293 There are a number of explanations for play behaviour in animals (reviewed in [47]),
294 but two hypotheses seem particularly pertinent to the acquisition of fighting technique. First,

295 the *motor training hypothesis* (MTH) posits that play promotes the adaptive development of
296 neuromuscular systems and (in vertebrates) the cerebellar synapses that allow for specific
297 motor patterns [48]. Here, play is expected to be concentrated during sensitive periods of
298 development. This type of play might also optimise the development of standard RHP traits,
299 such as strength and stamina, but if it promotes changes in synaptic connections it could also
300 allow for the development of technique. A second explanation for the function of play is the
301 *training for the unexpected hypothesis* (TUH) [47]. This includes situations where an animal
302 simply has to recover from losing its footing through to situations where an individual's
303 options are directly impacted by the unpredictable actions of others. For instance, Spinka et
304 al. [47] describe situations such as being “knocked over”, “pinned down” or “shaken
305 vigorously”, all of which might occur during a fight.

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

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

328

329

330 *Variation in skill*

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

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

358

359

360 **HOW COULD SKILL PROMOTE SUCCESSFUL FIGHTING?**

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

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

369 *Skill reveals underlying qualities*

370 During courtship, receivers of dynamic and repetitive signals (usually females) might be
371 interested in the level of skill displayed *per se*, since skilful behaviour may indicate the
372 underlying quality of the performer. Indeed, studies of sexual displays in birds [57,58] and
373 humans [59] indicate that the receivers of such signals are sensitive to this type of variation.
374 Signals that reveal underlying quality might also be pertinent during a fight between males if
375 the fight is observed by females that use information on skill to subsequently choose a mate
376 [56]. Similarly, if skilful agonistic behaviour correlates with persistence capacity or strength,
377 then skill could reveal information about RHP during contests settled through mutual
378 assessment [12]. On the other hand, contests can also involve costs that accrue to individuals
379 through the repeated performance of energetically challenging behaviour [13], as well as
380 costs that opponents inflict directly on one another through injuries [14]. Therefore, the level
381 of skill used in a fight could be important not only because skill *per se* is directly assessed by
382 a potential mate or a rival but also because skill level will influence the costs accrued through
383 performing agonistic behaviour and the costs that can be inflicted on the opponent.

384

385 *Efficiency and endurance*

386 Vigorous fighting involves the repetition of challenging behaviours, so performing these
387 motor patterns efficiently seems imperative. In the example of shell fighting in hermit crabs,
388 Briffa & Fortescue [34] quantified the motor patterns involved in individual raps by
389 measuring the distance through which the attacker's shell was displaced. As well as rapping
390 more vigorously than attackers that failed to evict the defender, successful attackers displaced

391 their shells through shorter distances and there was a negative correlation between
392 displacement distance and vigour. Over-displacement of the shell might have reduced the
393 capacity for vigorous rapping, possibly by wasting energy. Interestingly, sustaining low
394 displacement distance presented a stronger challenge to certain attackers. Those that evicted
395 the defender showed a gradual reduction in displacement as the fight progressed whereas
396 those that failed to evict the defender showed increasing displacement over the fight.
397 Although analyses of motor patterns during animal fights have rarely been undertaken,
398 similar approaches have been used to study human combat sports. Ashker [54] analysed the
399 proportion of punches on target over three-round boxing matches and found that although
400 winners fought with greater accuracy overall, for both winners and losers the proportion of on
401 target punches declined from round to round. These examples indicate that the ability to fight
402 skilfully (in terms of accuracy), as well as vigorously, is constrained by fatigue.

403

404 *Accuracy and damage*

405 Some fights involve inflicting direct blows on the opponent, which have the potential to
406 cause injury. Recipients of attempted blows would benefit from making rapid decisions on
407 appropriate defensive moves, such as evasion or blocking, that are executed accurately so as
408 to match the anticipated site of impact. For individuals attempting to strike the opponent the
409 accuracy of agonistic behaviour will determine their effectiveness, for instance by targeting
410 the most vulnerable part of the body. Furthermore, as inflicting damage has recently been
411 shown to sometimes result in injury to the attacker as well as the recipient [60], the ability to
412 effectively target attacks for maximum impact may reduce the costs incurred by the attacker.
413 Particularly in the Pancrustacea, self-inflicted damage costs could be avoided by the accurate
414 targeting of strikes on weakly armored, rather than strongly armored, regions of the

415 opponent's body (see [27]). Individuals that are better able to land targeted blows may also be
416 able to secure a victory through a single attack, whereas other less skillful fighters may have
417 to strike several times before causing the opponent to retreat. By deploying multiple attacks,
418 individuals not only increase the likelihood of sustaining substantial self-inflicted damage,
419 but also give their opponent the time and chance to strike back and thus may incur
420 even higher damage costs. Therefore skillful individuals could be able to win injurious fights
421 faster, by inflicting single blows with maximal impact and minimum cost.

422

423

424 *Appropriate choice of tactics*

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

434

435 *Skill and strategic decisions*

436 Thus far we have considered how skill may promote victory (i.e. act as an RHP trait) for
437 individuals committed to winning the contest in order to obtain a valuable resource. Under

438 certain circumstances, however, persisting in a contest through to victory may not be the
439 appropriate strategy, since fighting is costly and RV may not necessarily outbalance the costs
440 needed to secure victory. Animals that decide to enter into fights should place a high value on
441 the resource but the perceived balance between RV and costs could change as the fight
442 progresses. First, perceived RV could be updated during the fight, for instance in situations
443 where an intruder only comes into close contact with the resource once the fight is under way
444 as in hermit crabs fighting over shells [62] or guppies fighting over shelters [63]. The ability
445 to make such assessments can vary with experience [62, 63]. Second, for contests that
446 involve mutual assessment, the perceived costs of victory could be updated as more
447 information is revealed about the opponent. In such cases, where it becomes apparent that the
448 resource is not worth fighting for relative to the anticipated costs of victory, persisting in the
449 fight should not be the optimal strategy. Thus, as well as making appropriate tactical
450 decisions, about which agonistic behaviours to use, making appropriate strategic decisions to
451 ‘cut ones losses’ is also an ability that could increase with experience of real fights [62, 63].

452

453 **CONCLUSIONS AND FUTURE DIRECTIONS**

454 A popular approach to the study of animal fighting is to focus on morphological RHP traits
455 and performance capacities, coupled with analysis of contest duration and outcome. This
456 closely follows an established framework [9,10] for determining whether contests are settled
457 through mutual-or self-assessment. However, we have previously argued [10,11] that there is
458 much to gain from quantifying actual agonistic behaviours within fights, specifically by
459 investigating vigour. Here we suggest that in addition to vigour we should also attempt to
460 analyse skill. Like vigour, initial evidence shows that skill can drive outcomes and varies as
461 fights progress [34,54] and the pattern of change in skill within fights can differentiate

462 winners from losers [34]. A wide range of approaches could be taken to the study of skill in
463 animal contests and it is likely that the relevance of any one approach will vary greatly
464 between study species due to the diversity of fighting behaviour among animals [4]. For
465 example, complex and diverse song is known to correlate with success in male birds but
466 without knowledge of this aspect of their natural history variable song patterns could be
467 misinterpreted as lacking in precision. With this caution in mind, potential approaches to the
468 study of fighting skill include the following: Kinematic studies could characterise agonistic
469 behaviour in 3 dimensions [64] such that the spatial components of skill can be quantified.
470 One might then quantify between-fight variance in the aiming of blows or strikes to estimate
471 accuracy and within-fight variance to estimate precision. Two approaches could be taken to
472 disentangle skill from technique. First, measuring overall motor performance capacities in a
473 context other than fighting could be useful if it is reasonable to assume that these will
474 correlate with technique. Second, one might observe individuals across multiple fights, to
475 account for the influence of opponents [64]. Longitudinal studies could also be used to track
476 (or manipulate) play fighting and real fighting during ontogeny, especially in long lived
477 species, to test the idea that experience [hsu] allows the conversion of ability to technique.
478 Finally, studies of skill should ideally incorporate more traditional RHP measures (e.g. body
479 size) so that the relative contribution of skill can be assessed. An interesting question relates
480 to the possibility of alternative fighting phenotypes; might skill be more important for some
481 (e.g. smaller) individuals whilst other (e.g. larger) individuals can rely more on strength and
482 stamina?

483 Although some initial evidence is available, the contribution of skill to fight outcomes
484 and decision making during fights remains a largely open question. If fighting animals have
485 evolved to compete skilfully as well as vigorously then we should see variation in the
486 efficiency, accuracy, precision and appropriateness of agonistic behaviour between fight

487 outcomes (winners versus losers) and between individuals with different levels of experience
488 of fighting and different life history trajectories. .

489

490 **AUTHOR CONTRIBUTIONS**

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

492

493 **FUNDING**

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

496

497 **REFERENCES**

- 498 1. Byers J, Hebets E, Podos J. 2010 Female mate choice based upon male motor
499 performance. *Anim. Behav.* **79**, 771–778. (doi:10.1016/j.anbehav.2010.01.009)
- 500 2. Williams AM, Hodges NJ. 2005 Practice, instruction and skill acquisition in soccer:
501 Challenging tradition. *J. Sports Sci.* **23**, 637–650. (doi:10.1080/02640410400021328)
- 502 3. Vieira MC, Peixoto PEC. 2013 Winners and losers: a meta-analysis of functional
503 determinants of fighting ability in arthropod contests. *Funct. Ecol.* **27**, 305–313.
504 (doi:10.1111/1365-2435.12051)
- 505 4. Briffa M, Hardy ICW. 2013 Introduction to Animal Contests. In *Animal Contests* (eds
506 ICW Hardy, M Briffa), p. 357. Cambridge: Cambridge University Press.
- 507 5. Huntingford FA, Turner AK. 1987 *Animal Conflict*. London: Chapman and Hall.
- 508 6. Chamorro-Florescano IA, Favila ME, Macías-Ordóñez R. 2011 Ownership, size and
509 reproductive status affect the outcome of food ball contests in a dung roller beetle: when do
510 enemies share? *Evol. Ecol.* **25**, 277–289
- 511 7. Parker GA. 1974 Assessment strategy and the evolution of fighting behaviour. *J.*
512 *Theor. Biol.* **47**, 223–243. (doi:10.1016/0022-5193(74)90111-8)
- 513 8. Humphries EL, Hebblethwaite AJ, Batchelor TP, Hardy ICW. 2006 The importance
514 of valuing resources: host weight and contender age as determinants of parasitoid wasp
515 contest outcomes. *Anim. Behav.* **72**, 891–898. (doi:10.1016/j.anbehav.2006.02.015)
- 516 9. Arnott G, Elwood RW. 2009 Assessment of fighting ability in animal contests. *Anim.*
517 *Behav.* **77**, 991–1004. (doi:10.1016/j.anbehav.2009.02.010)
- 518 10. Briffa M, Elwood RW. 2009 Difficulties remain in distinguishing between mutual and
519 self-assessment in animal contests. *Anim. Behav.* **77**, 759–762.
520 (doi:10.1016/j.anbehav.2008.11.010)

- 521 11. Briffa M. 2015 Agonistic signals: Integrating analysis of functions and mechanisms.
522 In *Animal Signaling and Function, An Integrative Approach* (eds DJ Irschick, M Briffa, J
523 Podos), pp. 141–167. Hoboken: Wiley Blackwell.
- 524 12. Enquist M, Leimar O. 1983 Evolution of fighting behaviour: Decision rules and
525 assessment of relative strength. *J. Theor. Biol.* **102**, 387–410. (doi:10.1016/0022-
526 5193(83)90376-4)
- 527 13. Payne RJH, Pagel M. 1997 Why do animals repeat displays? *Anim. Behav.* **54**, 109–
528 19.
- 529 14. Payne RJH. 1998 Gradually escalating fights and displays: the cumulative assessment
530 model. *Anim. Behav.* **56**, 651–662.
- 531 15. Briffa M, Sneddon LU. 2007 Physiological constraints on contest behaviour. *Funct.*
532 *Ecol.* **21**, 627–637. (doi:10.1111/j.1365-2435.2006.01188.x)
- 533 16. Arnott G, Elwood RW. 2008 Information gathering and decision making about
534 resource value in animal contests. *Anim. Behav.* **76**, 529–542.
535 (doi:10.1016/j.anbehav.2008.04.019)
- 536 17. Fayed SA, Jennions MD, Backwell PRY. 2008 What factors contribute to an
537 ownership advantage? *Biol. Lett.* **4**, 143–145. (doi:10.1098/rsbl.2007.0534)
- 538 18. Briffa M, Hardy ICW, Gammell MP, Jennings DJ, Clarke DD, Goubault M. 2013
539 Analysis of contest data. In *Animal Contests* (eds ICW Hardy, M Briffa), pp. 47–85.
540 Cambridge: Cambridge University Press.
- 541 19. Petersen G, Hardy ICW. 1996 The importance of being larger: parasitoid intruder –
542 owner contests and their implications for clutch size. *Anim. Behav.* **51**, 1363–1373.
543 (doi:10.1006/anbe.1996.0139)
- 544 20. Sneddon LU, Huntingford FA, Taylor AC. 1997 Weapon size versus body size as a
545 predictor of winning in fights between shore crabs, *Carcinus maenas* (L.). *Behav. Ecol.*
546 *Sociobiol.* **41**, 237–242. (doi:10.1007/s002650050384)
- 547 21. Judge KA, Bonanno VL. 2008 Male weaponry in a fighting cricket. *PLoS One* **3**,
548 e3980. (doi:10.1371/journal.pone.0003980)
- 549 22. Claverie T, Smith IP. 2007 Functional significance of an unusual chela dimorphism in
550 a marine decapod: specialization as a weapon? *Proc. Biol. Sci.* **274**, 3033–8.
551 (doi:10.1098/rspb.2007.1223)
- 552 23. Mowles SL, Cotton PA, Briffa M. 2010 Whole-organism performance capacity
553 predicts resource-holding potential in the hermit crab *Pagurus bernhardus*. *Anim. Behav.* **80**.
554 (doi:10.1016/j.anbehav.2010.05.004)
- 555 24. Briffa M, Elwood RW. 2004 Use of energy reserves in fighting hermit crabs. *Proc. R.*
556 *Soc. B Biol. Sci.* **271**, 373–379. (doi:10.1098/rspb.2003.2633)

- 557 25. Seebacher F, Wilson RS. 2006 Fighting fit: thermal plasticity of metabolic function
558 and fighting success in the crayfish *Cherax destructor*. *Funct. Ecol.* **20**, 1045–1053.
559 (doi:10.1111/j.1365-2435.2006.01194.x)
- 560 26. Haley MP. 1994 Resource-holding power asymmetries, the prior residence effect, and
561 reproductive payoffs in male Northern elephant seal fights. *Behav. Ecol. Sociobiol.* **34**, 427–
562 434. (doi:10.1007/BF00167334)
- 563 27. Palaoro A V., Briffa M. 2017 Weaponry and defenses in fighting animals: how
564 allometry can alter predictions from contest theory. *Behav. Ecol.* **28**, 328–336.
565 (doi:10.1093/beheco/arw163)28. McCullough EL. 2014 Mechanical limits to maximum
566 weapon size in a giant rhinoceros beetle. *Proc. R. Soc. B* **281**, 20140696.
567 (doi:10.1098/rspb.2014.0696)
- 568 29. Maynard Smith J, Parker GA. 1976 The logic of asymmetric contests. *Anim. Behav.*
569 **24**, 159–175. (doi:10.1016/S0003-3472(76)80110-8)
- 570 30. Jennings DJ, Gammell MP, Payne RJH, Hayden TJ. 2005 An investigation of
571 assessment games during fallow deer fights. *Ethology* **111**, 511–525. (doi:10.1111/j.1439-
572 0310.2005.01068.x)
- 573 31. Hardy ICW. 1998 Butterfly battles: On conventional contests and hot property.
574 *Trends Ecol. Evol.* **13**, 385–386. (doi:10.1016/S0169-5347(98)01430-X)
- 575 32. Mowles SL, Ord TJ. 2012 Repetitive signals and mate choice: Insights from contest
576 theory. *Anim. Behav.* **84**, 295–304. (doi:10.1016/j.anbehav.2012.05.015)
- 577 33. Earley RL, Hsu Y. 2013 Contest behaviour in fishes. In *Animal Contests* (eds ICW
578 Hardy, M Briffa), pp. 199–227. Cambridge: Cambridge University Press.
- 579 34. Briffa M, Fortescue KJ. 2017 Motor pattern during fights in the hermit crab *Pagurus*
580 *bernhardus* : evidence for the role of skill in animal contests. *Anim. Behav.* **128**, 13–20.
581 (doi:10.1016/j.anbehav.2017.03.031)
- 582 35. Briffa M, Elwood RW, Russ JM. 2003 Analysis of multiple aspects of a repeated
583 signal: power and rate of rapping during shell fights in hermit crabs. *Behav. Ecol.* **14**, 74–79.
584 (doi:10.1093/beheco/14.1.74)
- 585 36. Briffa M, Elwood RW, Dick J. 1998 Analysis of repeated signals during shell fights
586 in the hermit crab *Pagurus bernhardus*. *Proc. R. Soc. B Biol. Sci.* **265**, 1467–1474.
587 (doi:10.1098/rspb.1998.0459)
- 588 37. Briffa M, Elwood RW. 2000 Analysis of the finescale timing of repeated signals: does
589 shell rapping in hermit crabs signal stamina? *Anim. Behav.* **59**, 159–165.
590 (doi:10.1006/anbe.1999.1273)
- 591 38. Guilford T, Dawkins MS. 1991 Receiver psychology and the evolution of animal
592 signals. *Anim. Behav.* **42**, 1–14. (doi:10.1016/S0003-3472(05)80600-1)
- 593 39. Green PA, Patek SN. 2015 Contests with deadly weapons: telson sparring in mantis
594 shrimp (Stomatopoda). *Biol. Lett.* **11**, 20150558. (doi:10.1098/rsbl.2015.0558)

- 595 40. Thach WT. 2014 Does the cerebellum initiate movement? *Cerebellum*. **13**, 139–150.
596 (doi:10.1007/s12311-013-0506-7)
- 597 41. Suthers RA, Margoliash D. 2002 Motor control of birdsong. *Curr. Opin. Neurobiol.*
598 **12**, 684–690. (doi:10.1016/S0959-4388(02)00386-0)
- 599 42. Stollewerk A. 2016 A flexible genetic toolkit for arthropod neurogenesis. *Philos.*
600 *Trans. R. Soc. B Biol. Sci.* **371**, 20150044. (doi:http://dx.doi.org/10.1098/rstb.2015.0044)
- 601 43. Wang VY, Zoghbi HY. 2001 Genetic regulation of cerebellar development. *Nat. Rev.*
602 *Neurosci.* **2**, 484–491. (doi:10.1038/35081558)
- 603 44. Shaw K, Wiley C. 2010 The genetic basis of behavior. In *Evolutionary Behavioral*
604 *Ecology* (eds D Westneat, C Fox), pp. 71–80. New York: Oxford University Press.
- 605 45. Boake CRB. 1989 Repeatability - Its Role in Evolutionary Studies of Mating-
606 Behavior. *Evol. Ecol.* **3**, 173–182. (doi:10.1007/Bf02270919)
- 607 46. Royle NJ, Lindström J, Metcalfe NB. 2005 A poor start in life negatively affects
608 dominance status in adulthood independent of body size in green swordtails *Xiphophorus*
609 *helleri*. *Proc. Biol. Sci.* **272**, 1917–22. (doi:10.1098/rspb.2005.3190)
- 610 47. Špinka M, Newberry RC, Bekoff M. 2001 Mammalian play: training for the
611 unexpected. *Q. Rev. Biol.* **76**, 141–68.
- 612 48. Byers JA, Walker C. 1995 Refining the motor training hypothesis for the evolution of
613 play. *Am. Nat.* **146**, 25–40. (doi:10.1086/285785)
- 614 49. Pellis SM. 1988 Agonistic versus amicable targets of attack and defense:
615 Consequences for the origin, function, and descriptive classification of play-fighting.
616 *Aggress. Behav.* **14**, 85–104. (doi:10.1002/1098-2337(1988)14:2<85::AID-
617 AB2480140203>3.0.CO;2-5)
- 618 50. Held SDE, Špinka M. 2011 Animal play and animal welfare. *Anim. Behav.* **81**, 891–
619 899. (doi:10.1016/j.anbehav.2011.01.007)
- 620 51. Hsu Y, Lee IH, Lu CK. 2009 Prior contest information: Mechanisms underlying
621 winner and loser effects. *Behav. Ecol. Sociobiol.* **63**, 1247–1257. (doi:10.1007/s00265-009-
622 0791-9)
- 623 52. Kim T, Zuk M. 2000. The effects of age and previous experience on social rank in
624 female red junglefowl, *Gallus gallus spadiceus*. *Anim. Behav.* **60**, 239–244.
- 625 53. Briffa M, Sneddon LU, Wilson AJ. 2015 Animal personality as a cause and
626 consequence of contest behaviour. *Biol. Lett.* **11**, 20141007. (doi:10.1098/rsbl.2014.1007)
- 627 54. El Ashker S. 2011. Technical and tactical aspects that differentiate winning and losing
628 performances in boxing. *Int. J. Perform. Anal. Sport* **11**, 356–364.
- 629 55. Carere C, Locurto C. 2011 Interaction between animal personality and animal
630 cognition. *Curr. Zool.* **57**, 491–498. (doi:10.1093/czoolo/57.4.491)56. Byers JA, Moodie

631 JD, Hall N. 1994 Pronghorn females choose vigorous mates. *Anim. Behav.* **47**, 33–43.
632 (doi:10.1006/anbe.1994.1005)

633 57. Manica LT, Macedo RH, Graves JA, Podos J. 2017 Vigor and skill in the acrobatic
634 mating displays of a Neotropical songbird. *Behav. Ecol.* **28**, 164–173.
635 (doi:10.1093/beheco/arw143)

636 58. Barske J, Schlinger BA, Wikelski M, Fusani L. 2011 Female choice for male motor
637 skills. *Proc. Biol. Sci.* **278**, 3523–8. (doi:10.1098/rspb.2011.0382)

638 59. Neave N, McCarty K, Freynik J, Caplan N, Hönekopp J, Fink B. 2011 Male dance
639 moves that catch a woman’s eye. *Biol. Lett.* **7**, 221–4. (doi:10.1098/rsbl.2010.0619)

640 60. Lane SM, Briffa M. 2017 The price of attack: rethinking damage costs in animal
641 contests. *Anim. Behav.* **126**. (doi:10.1016/j.anbehav.2017.01.015)

642 61. Edmonds E, Briffa M. 2016 Weak rappers rock more: Hermit crabs assess their own
643 agonistic behaviour. *Biol. Lett.* **12**. (doi:10.1098/rsbl.2015.0884)

644 62. Doake S, Elwood RW. 2011. How resource quality differentially affects motivation
645 and ability to fight in hermit crabs. *Proc. R. Soc. Lond. B Biol Sci.* **22**, 567-573.

646 63. McCallum ES, Gulas ST, Balshine S. 2017. Accurate resource assessment requires
647 experience in a territorial fish. *Anim. Behav.* **123**, 249-527. (doi:
648 10.1016/j.anbehav.2016.10.032)

649 63. Hedrick TL. 2008 Software techniques for two- and three-dimensional kinematic
650 measurements of biological and biomimetic systems. *Bioinspir. Biomim.* **3**, 34001.
651 (doi:10.1088/1748-3182/3/3/034001)

652

653 64. Wilson AJ, de Boer M, Arnott G, Grimmer A. 2011. Integrating personality research
654 and animal contest theory: aggressiveness in the green swordtail *Xiphophorus helleri*. *PLoS*
655 *One* **6**, e28024. (doi:10.1371/journal.pone.0028024).

656 . Hsu Y, Earley RL, Wolf LL. 2006 Modulation of aggressive behaviour by fighting
657 experience: mechanisms and contest outcomes. *Biol. Rev. Camb. Philos. Soc.* **81**, 33–74.
658 (doi:10.1017/S146479310500686X)

659

660

661

662 **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

663

664

665

666

667

668

669

670

671

672

673

674 **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

675

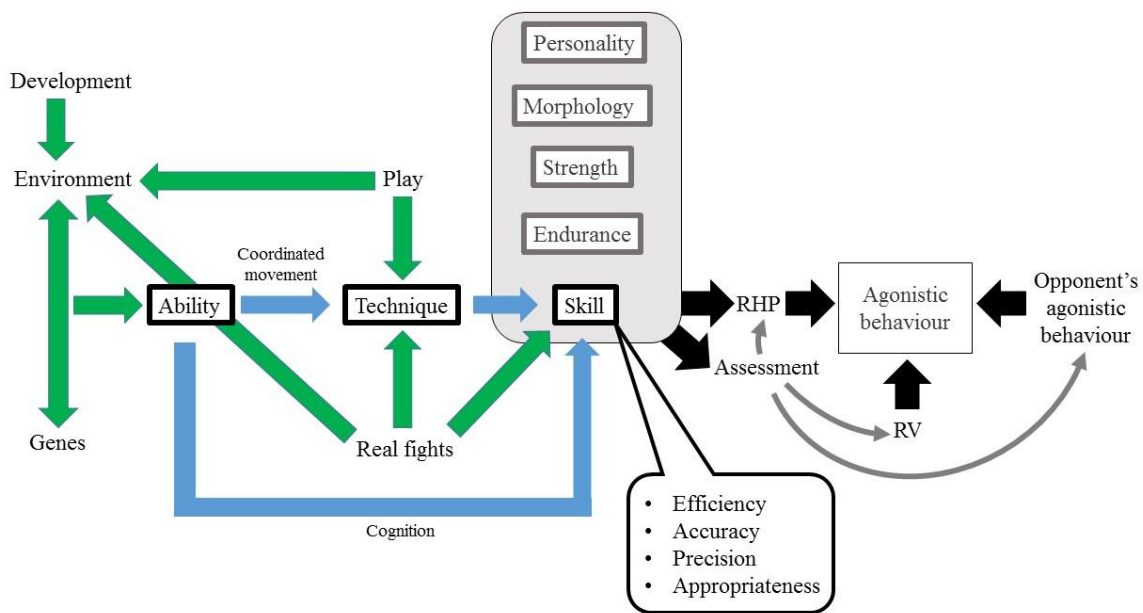


Figure 1: Schematic representation of relationships between ability, skill and technique, applied to animal contests. In sports opponents try to thwart one another's attempts to win and in sports training it is therefore necessary to distinguish between innate ability, technique in the absence of significant 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.