

2017-04-01

# The price of attack: Rethinking damage costs in animal contests

Lane, Sarah

<http://hdl.handle.net/10026.1/8565>

---

10.1016/j.anbehav.2017.01.015

Animal Behaviour

Elsevier BV

---

*All content in PEARL is protected by copyright law. Author manuscripts are made available in accordance with publisher policies. Please cite only 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 PRICE OF ATTACK: RETHINKING DAMAGE COSTS IN ANIMAL CONTESTS**

2

3 **Sarah M. Lane\* & Mark Briffa**

4 Marine biology and ecology research centre, Plymouth University, Drake Circus, Plymouth,  
5 UK, PL4 8AA

6 \*Correspondence: Sarah M. Lane, Davy 620, Marine biology and ecology research centre,  
7 Plymouth University, Drake Circus, Plymouth, UK, PL4 8AA

8 E-mail: [sarah.lane@plymouth.ac.uk](mailto:sarah.lane@plymouth.ac.uk); Contact phone number: 01752 584618

9

10 **Theoretical models of injurious animal contests, such as the cumulative assessment model**  
11 **(CAM) predict that an individual's decision to give up and retreat from a fight is**  
12 **determined by reaching a maximum cost threshold ( $C_{max}$ ). Under this model, an individual**  
13 **gives up when the accumulated costs of persisting exceed this threshold. CAM predicts**  
14 **that the velocity with which  $C_{max}$  is reached depends on both the energetic (physiological)**  
15 **costs of remaining in the fight and the damage costs of injuries received. Here we propose**  
16 **that damage costs are not only accumulated by receiving injuries, but in some cases also**  
17 **by inflicting injury (attacking). We argue that these self-inflicted damage costs need to be**  
18 **incorporated into theoretical frameworks in order to fully understand what drives an**  
19 **individual to make the decision to give up and call for further research into this area.**

20

21 **Keywords:** animal contests; cumulative assessment model; damage costs; injurious contests;  
22 self-inflicted damage

23

24 Before the introduction of gloves around 1897, there were no recorded deaths in  
25 professional boxing. This is because a human hand will break on impact with a human skull  
26 long before the skull does. Thanks to boxing gloves, “boxer’s fracture” (the breakage of the  
27 metacarpal bones on impact with an immovable object) is now restricted to emergency  
28 department waiting rooms after brawls in bars, whilst 3 to 4 professional fights end in a  
29 death every year in the USA alone and 15% of professional fighters suffer permanent brain  
30 injury during their career (Ryan, 1987; 1991). Gloves have thus enabled boxers to inflict  
31 injury whilst avoiding the self-inflicted injuries that would otherwise accrue from punching  
32 an opponent.

33 In many models of animal contest theory, the costs of entering and persevering in a  
34 fight are split into two separate components: - energetic costs ( $E$ ) which push an individual  
35 towards fatigue (such as the use of energy reserves, oxygen consumption or the build-up of  
36 metabolic waste products) and damage costs ( $D$ ), the physical injuries received by an  
37 individual as a result of its opponent’s agonistic behaviour. Damage costs accumulated  
38 during fights in both human and animal contests are generally thought of in terms of the  
39 recipient of agonistic behaviour (e.g. the boxer receiving the blow to the head). Theoretical  
40 models of animal contests which account for damage received in injurious fights, in  
41 particular the cumulative assessment model (CAM), assume that individual contestants  
42 possess a maximum cost threshold ( $C_{\max}$ ), which once reached triggers the individual to give  
43 up and withdraw from the contest. CAM predicts that the time taken for an individual to  
44 reach  $C_{\max}$  will be negatively correlated with both the energetic costs of remaining in the  
45 fight ( $E$ ) and the amount of damage caused to the focal individual by its opponent ( $D$ )

46 (Payne, 1998). The higher the accumulated costs, the sooner  $C_{max}$  will be reached and the  
47 sooner the loser will retreat.

$$48 \qquad C_{accumulated} = E + D \qquad (1)$$

49 Giving up is triggered when: -

$$50 \qquad C_{accumulated} > C_{max} \qquad (2)$$

51 CAM assumes that an individual's contest decisions are based upon self-assessment but  
52 recognises that the actions of the opponent (i.e. attacks) can impact the speed at which an  
53 individual reaches  $C_{max}$ . However, while the CAM includes the energetic costs of performing  
54 agonistic behaviour, it does not take into account the potential self-inflicted damage costs  
55 of carrying out agonistic behaviour. In fact to date, to our knowledge, self-inflicted damage  
56 has not been considered as a cost of fighting in animal contest literature.

57 The CAM assumes that injuries inflicted are costly only to the recipient and not the  
58 attacker, but as we have already seen from our boxing example, such assumptions do not  
59 necessarily hold true. Thus in situations where agonistic behaviour damages the actor as  
60 well as the recipient, damage costs will accrue not only through the agonistic actions of  
61 one's opponent but also through one's own agonistic actions, which we refer to as self-  
62 inflicted damage ( $D_{SI}$ ). Thus the total costs accrued are the sum of energy expended,  
63 damage inflicted by the opponent and damage that is self-inflicted through the focal  
64 individual's own agonistic behaviour.

$$65 \qquad C_{accumulated} = E + D + D_{SI} \qquad (3)$$

66 A range of properties of  $D_{SI}$  will determine its average contribution to C accumulated.  
67 Essentially, self-inflicted damage will reduce the differential of damage costs between the  
68 recipients and inflictors of injurious agonistic behaviour, compared with a scenario where  
69 self-inflicted damage is absent. Under the predictions of the CAM, Payne (1998) argues that  
70 unlike energetic costs damage costs come from an external source and are thus out of the  
71 recipient's control, but in cases with self-inflicted damage, a significant proportion of the  
72 total damage costs are under the control of the recipient. Specifically, the attacker has the  
73 potential to control the amount of  $D_{SI}$  experienced by adjusting the rate and power of attack.  
74 In species that do not exhibit variation in the power exerted in attacks, only the rate of  
75 attack will be important in determining  $D_{SI}$ , for example in the beadlet sea anemone *Actinia*  
76 *equina*, the number of attacks is functionally correlated with the amount of  $D_{SI}$  experienced  
77 by the attacker. In other species, such as musk ox (*Ovibos moschatus*) the power of attack is  
78 more important in determining victory and has a much greater effect than attack rate on  
79 the severity of  $D_{SI}$  (Wilkinson & Shank, 1976). Furthermore, in their 1981 paper, Parker and  
80 Rubenstein assume energetic costs to be equally incurred by both opponents but damage  
81 costs to be sustained only by the loser/recipient, but again when self-inflicted damage is a  
82 feature of injurious fighting, this latter assumption would not hold. Rather, in injurious fights  
83 damage costs may be incurred by both winners and losers, even in examples where it is only  
84 winners that perform the injurious behaviours.

85

## 86 **EVIDENCE OF SELF-INFLICTED DAMAGE VIA ATTACKS IN NONHUMAN ANIMALS**

87 Evidence of self-inflicted damage in attackers is limited, likely in part due to the simple fact  
88 that until now damage costs have only been explicitly considered for the recipients of

89 attacks. However, the evidence that does exist illustrates that self-inflicted damage varies  
90 along three different axes; likelihood, severity and reversibility (table 1). While it is  
91 important to remember that not all fights escalate into injurious attacks, being settled using  
92 non-injurious displays or trials of strength, here we define likelihood as the probability that  
93  $D_{SI}$  will occur if an injurious attack is used. At one extreme, self-inflicted damage during an  
94 attack is unavoidable, as it is functionally linked to the use of weapons. In other cases, and  
95 perhaps more generally,  $D_{SI}$  during an attack is a risk but not a certainty. Severity is the loss  
96 of fitness resulting from (a) loss of function due to  $D_{SI}$  from the time of attack until healing is  
97 complete and (b) costs allocated to the healing process. Reversibility (arguably a component  
98 of severity) is the potential/capacity for the self-inflicted injury to heal - i.e. completely,  
99 incompletely or not at all – over the lifetime of the recipient. The severity and reversibility of  
100 the damage again vary depending upon the species and/or context, the most extreme  
101 examples resulting in (naturally irreversible) death. All three axes of self-inflicted damage  
102 will impact an individual's decision to give up within the timescale of a fight. Note that  
103 severity and reversibility should also pertain to damage inflicted by the opponent, although  
104 these features are rarely assessed in empirical studies (a notable exception is the system  
105 developed by Murray, 1987 for scoring injury severity in fig wasp contests). In contrast, the  
106 likelihood of damage if an injurious tactic is used is a specific feature of  $D_{SI}$ .

107           In this section we will review examples of self-inflicted damage to attackers available  
108 in the current literature and discuss these examples in terms of the three axes outlined  
109 above.

110

111 *Self-inflicted damage in dyadic contests*

112 Thus far the most well-described and extreme example of self-inflicted damage to attackers  
113 is found in contests between beadlet sea anemones *Actinia equina*. *A. equina* are among the  
114 simplest animals to engage in contests. They lack a centralised nervous system but possess  
115 weapons in the form of specialised stinging tentacles called acrorhagi which contain high  
116 concentrations of stinging nematocytes and are used solely for fighting other anemones  
117 (Williams, 1978; Brace, Pavey, & Quickie, 1979; Bigger, 1982). During contests, anemones  
118 scrape inflated acrorhagi along their opponent's body column. Pieces of the attacker's  
119 nematocyte-filled acrorhagial ectoderm (known as "peels") stick to the recipient of the  
120 attack causing localised necroses (Nüchter, Benoit, Engel, Ozbek, & Holstein, 2006; Bartosz,  
121 Finkelshtein, Przygodzki, Bsoor, Neshor, Sher, & Zlotkin, 2008) whilst the attacking anemone  
122 is left with holes in its acrorhagi (figure 1). The greater the number of peels landed, the  
123 more damage done to the recipient and the greater chance of winning for the attacker  
124 (Rudin & Briffa, 2011). However in *A. equina*, individuals are unable to damage their  
125 opponents without also damaging themselves, and an increase in peels means an increase  
126 in damage to the attacker by necessity. Furthermore, while healing appears to be relatively  
127 rapid (< 7 days – SML personal observation) the accumulated costs of damage are unlikely  
128 to be immaterial, especially in fights in which both individuals receive and inflict attacks.  
129 Thus in *A. equina* the velocity at which  $C_{max}$  is reached will be reliant upon the energetic  
130 costs of remaining in the contest, the number of peels received *and* the number of peels  
131 inflicted. The relative costs of receiving and inflicting peels may of course not be identical, in  
132 which case the two kinds of damage costs may make different contributions to  $C_{max}$ . For  
133 instance, the physical damage caused by receiving and inflicting peels presumably leaves  
134 individuals at greater risk of infection from pathogens until healing is complete (although  
135 interestingly, the mucus produced by *A. equina* has recently been shown to have

136 antibacterial properties, potentially staving off infection, Stabili, Schirosi, Parisi, Piraino, &  
137 Cammarata, 2015). Inflicting peels brings about an additional cost by damaging acrorhagi,  
138 and thus rendering weapons unavailable for future contests until fully healed.

139           Less extreme (in terms of likelihood, severity and reversibility) examples of self-  
140 inflicted damage during contests have been noted in beetles, elk and deer. The physiological  
141 cost of antler production in cervids is known to be extremely high (e.g. causing seasonal  
142 osteoporosis Banks, Epling, Kainer, & Davis, 1968) in contrast to the relative inexpense of  
143 beetle horns (McCullough & Emlen, 2013; McCullough & Tobalske, 2013), but both weapons  
144 run the risk of breakage during a contest (Figure 1). Rhinoceros beetles in particular possess  
145 a vast array of exaggerated horn structures for use in fighting. While self-inflicted damage to  
146 the attacker is not certain in these species, a recent study of the Asian rhinoceros beetle  
147 *Trypoxylus dichotomus* has shown that it is still a significant risk (with ~21% of males within  
148 a population showing some level of horn damage) and that furthermore, the likelihood of  
149 horn breakage increases with horn size (McCullough, 2014). In fallow deer, major antler  
150 damage (e.g. damage to the antler palm and/or beam) is associated with the agonistic  
151 behaviour of the individual, specifically pushing and jump clashes, suggesting that this  
152 damage may be the result of both the focal individual's behaviour *and* that of its opponent  
153 (D. Jennings, personal communication, 3 November 2016). Similarly in tule elk *Cervus*  
154 *elaphus nannodes*, antler breakage is seen in more than 80% of rutting males (Johnson,  
155 Bleich, Krausman, & Koprowski, 2007). Bulls and bucks moult and regrow their antlers every  
156 season, meaning that any damage received will be repaired before the next rutting season  
157 and antler damage in elk has been shown to have little impact on the fighting success of  
158 individuals within a season (Johnson et al., 2007). Rhinoceros beetles on the other hand are



159 unable to repair horns once they are broken (i.e. the damage is irreversible), rendering  
160 males unable to secure access to females and thus eliminating any possible future mating  
161 success. Thus, the costs arising from the three axes of probability, severity and reversibility  
162 of self-inflicted damage will vary across species. Nevertheless, it seems probable that this  
163 form of damage is important in many cases where weapons are used. A final potential  
164 example of  $D_{SI}$  in animal contests has been observed in bethylid parasitoid wasps. In a small  
165 percentage of contests, losers release a volatile chemical before fleeing rapidly, leaving the  
166 winner exposed to this chemical in the confined contest arena (Goubault, Batchelor,  
167 Linforth, Taylor, & Hardy, 2006; Goubault et al., 2008). The chemical is only ever released by  
168 the loser and is known to be insecticidal to some organisms. It is thought to act as a  
169 rearguard weapon, enabling the retreat of the loser while damaging the winner. However,  
170 the question remains as to why losers only emit this chemical infrequently. One possibility is  
171 that it is costly to produce, but another is that this chemical weapon is injurious both to the  
172 winner and to the loser who emits it, an explanation that could also account for the loser's  
173 swift exit (I. C. W. Hardy, personal communication, 5 January 2017).

174

#### 175 *Self-inflicted damage during colony defence: social insects*

176 With such a paucity of information on the damage to attackers during animal contests we  
177 now turn to an especially striking example of self-destructive attacks, suicidal colony  
178 defence in social insects. While it must be remembered that these examples do not strictly  
179 adhere to the rules of dyadic contests (although see Batchelor & Briffa, 2010; 2011 and  
180 Batchelor, Santini, & Briffa, 2012), no discussion of self-inflicted damage would be complete  
181 without mentioning this most extreme phenomenon. Social insects demonstrate an

182 incredible variety of suicidal defences ranging from biting, to stinging, to autothysis (suicide  
183 via internal rupturing/explosion). For example on coming into contact with intruders within  
184 the colony (and in some examples outside of the colony), resident workers of the stingless  
185 bee *Trigona hyalinata* approach the intruder, bite them and do not disengage, resulting in  
186 the death of the attacker (Shackleton, Toufalia, Balfour, Nascimento, Alves &  
187 Ratnieks, 2015). Similarly carpenter ant *Camponotus (Colobopsis) cylindricus* and gall-  
188 forming aphid *Quadrartus yoshinomyai* workers secrete an adhesive corrosive substance,  
189 sticking to intruders and once again choosing death over detachment (Davidson, Lessard,  
190 Bernau, & Cook, 2007; Davidson, Kamariah, & Billen, 2011; Shorter & Rueppell, 2015). The  
191 difference between inter-colony aggression in social insects and dyadic encounters in other  
192 animals, of course, is that the costs accrue to colonies rather than individuals. Nevertheless,  
193 it seems clear that groups of fighting animals can suffer self-inflicted damage analogous to  
194 that experienced by fighting individuals.

195

## 196 **EVIDENCE OF SELF-INFLICTED DAMAGE VIA ATTACKS IN HUMANS**

197 Self-inflicted damage to attackers in human contests is seen in a variety of contexts. Perhaps  
198 the most obvious source of  $D_{SI}$  comes from fighting sports. As discussed earlier, brain  
199 injuries and deaths would not be components of boxing were it not for the introduction of  
200 gloves (Ryan, 1987; 1991). The public desire for less bloody fights and more dramatic  
201 knockouts drove the eradication of bare-knuckle fighting and with it “boxer’s fracture”,  
202 instead leading to a much more lethal sport. In fact, the use of protective gear has increased  
203 injury prevalence in many sports due to the phenomena of ‘risk homeostasis’, in which the  
204 presence of protective gear promotes a decreased perception of risk, causing individuals to

205 take more risks and behave more aggressively, thus ironically resulting in higher levels of  
206 injury than in the absence of protective gear (Wilde, 1988). For instance, a research  
207 programme set up to investigate how the implementation of helmetless-tackle training  
208 could help decrease the occurrence of head impacts in American football (an individual  
209 college football player can experience 1000 head impacts in a single season, Crisco et al.,  
210 2010) found that within one season of helmetless training, the number of head impacts  
211 decreased by 28% compared with that of a helmeted control group (Swartz et al., 2015).  
212 Further examples of attackers sustaining injuries in professional sports have been seen in  
213 judo, where throwing your opponent is a major means of attack. A paper reporting the  
214 effects of various fight-sustained injuries on future contest performance identified  
215 attempting a throw as one of the most common situations in which strain injuries occurred  
216 (Green, Petrou, Forgarty-Hover, & Rolf, 2007).

217           Self-inflicted damage to human attackers is not just limited to sport, examples can  
218 be found in the tactics and weapons used during interstate wars and violent crime. The use  
219 of chemical weapons in warfare comes with a whole host of risks to the soldiers given the  
220 responsibility of deploying them. Data in such a sensitive area is hard to come by, but  
221 medical records from World War I indicate that the first use of chlorine gas by German  
222 soldiers resulted in a large number of cases of permanent pulmonary damage alongside a  
223 death rate of ~5% in their own men. At the time, soldiers were simply given damp cloths to  
224 cover their faces and the risk of chlorine exposure depended entirely upon which way the  
225 wind was blowing (Hurst, 1917; Szincz, 2005). Furthermore, some methods of attack are  
226 self-sacrificial by nature, such as the kamikaze attacks implemented by the Japanese military  
227 in World War II and more recently the suicide bombings carried out globally by terrorists.

228 Finally, evidence from forensic analyses have shown that (accidental) self-wounding is  
229 commonplace in assailants during stabbing attacks, so much so that the type of wounds  
230 found on the assailant can be linked back to the murder weapon (Varnon, Courtney, & Ekis,  
231 1995) and help secure a conviction.

232

### 233 **IMPLICATIONS FOR ANIMAL CONTEST THEORY AND ANALYSIS**

234 To date, neither theoretical nor empirical studies have considered self-inflicted damage, yet  
235 the existence of  $D_{SI}$  has many implications for animal contest theory and the way we  
236 interpret and analyse contest dynamics, specifically what determines which individual gives  
237 up and when. Under the CAM, an individual can nudge its opponent closer towards its giving  
238 up threshold ( $C_{max}$ ) by inflicting attacks. But when inflicting damage is associated with  $D_{SI}$ , by  
239 attacking its opponent, an individual also nudges itself closer to its own  $C_{max}$ . Thus, the  
240 differential between damage inflicted on an opponent and  $D_{SI}$  is critical in determining  
241 which individual withdraws first from an injurious fight. The ratio between the amount of  
242 damage inflicted and  $D_{SI}$  (hereafter  $D:D_{SI}$ ) will have implications for contest duration both  
243 within and between species. Within species, some individuals may be able to inflict damage  
244 while minimising the amount of  $D_{SI}$  they experience. For others, the margin between what  
245 they inflict and self-inflict will be lower, meaning that they can only inflict a limited amount  
246 of damage on their opponent before hurting themselves. Variation in  $D:D_{SI}$  may be brought  
247 about by simple variation in morphology, specifically weaponry, making some individuals  
248 more susceptible to  $D_{SI}$  than others. For instance Asian rhinoceros beetles with larger horns  
249 are able to inflict more damage than their smaller counterparts, but due to mechanical  
250 limits on horn size, larger horns are more likely to snap in the process (McCullough, 2014).

251 Thus, although individuals with larger horns may be able to elicit more damage in a single  
252 attack, individuals with smaller horns are able to inflict damage for longer before damaging  
253 themselves. Furthermore, some individuals may be able to inflict more damage without  
254 hurting themselves not due to morphological differences, but rather differences in skill,  
255 being better able to land an attack without injuring themselves. Skilful individuals may also  
256 be better able to successfully land a single blow, securing a victory without having to strike  
257 repeatedly, a skill which would be of particular importance in situations where  $D_{SI}$  increases  
258 with attack rate. Individuals who possess a high  $D:D_{SI}$  ratio (e.g. 6:1) will be able to inflict a  
259 greater amount of damage to their opponent before reaching their maximum cost threshold  
260 ( $C_{max}$ ) and thus be more likely to win contests in which victory relies upon attack rate and/or  
261 power.

262 The  $D:D_{SI}$  differential will likely vary across as well as within species. In species in  
263 which the risk of  $D_{SI}$  is very low, the ability to damage an opponent may be very important in  
264 comparison to species in which the risk of  $D_{SI}$  is high. Of course, the rate at which  $C_{max}$  is  
265 reached will still be dependent upon damage costs inflicted on individuals by their opponent  
266 and thus the  $D:D_{SI}$  ratio of an individual's opponent will also affect the velocity with which  
267  $C_{max}$  is reached and therefore who gives up first. In species with a low risk of  $D_{SI}$  (and in  
268 contests between opponents with disparate  $D:D_{SI}$  ratios), contest duration will be negatively  
269 correlated with winner RHP (resource holding potential). The higher winner RHP, the more  
270 injuries the winner will be able to inflict on its opponent before reaching its own  $C_{max}$  and  
271 the quicker its opponent will be to retreat (leading to problems distinguishing between  
272 mutual and self-assessment as discussed by Briffa & Elwood, 2009; see also Palaoro and  
273 Briffa 2016 for a consideration of how the allometric growth of weapons and defences may

274 complicate our ability to distinguish between mutual- and self-assessment). But if damage  
275 inflicted and  $D_{SI}$  are very closely linked, then damage inflicted in a fight may become less  
276 relevant for fight outcome and the link between absolute RHP and contest duration less  
277 clear. Furthermore in species in which the risk of  $D_{SI}$  is high, contests may be over faster  
278 than in species with a lower  $D_{SI}$  risk, especially in contests with mutual attacks, in which the  
279 costs of self-inflicted damage are combined with the costs of receiving damage, pushing  
280 individuals faster towards their  $C_{max}$ .

281           To this day, many empirical studies of contest behaviour base their questions and  
282 predictions on the classic Hawk-Dove model of John Maynard Smith and Geoff Parker (1976).  
283 This model assumes that the evolution and prevalence of restraint (non-injurious fighting) is  
284 due to negative frequency dependent selection acting on fighting strategies and the cost of  
285 injurious fighting ( $C$ ) usually far outweighing the value of the contested resource. Under the  
286 Hawk-Dove model, the only cost of fighting is that of receiving injuries from the actions of  
287 an opponent, but what happens when we factor in the additional cost of inflicting injuries?  
288 Perhaps the most obvious consequence of incorporating  $D_{SI}$  into the Hawk-Dove model is  
289 that it increases  $C$ , making the evolution of injurious fighting even less likely. However, the  
290 extent to which  $D_{SI}$  contributes to  $C$  will depend on the damage to  $D_{SI}$  ratio. When damage  
291 and  $D_{SI}$  are very closely linked (e.g. 1:1), the cost of self-inflicted damage will (at some  
292 threshold ratio) outweigh the benefits of damaging an opponent, such that inflicting  
293 damage is no longer worthwhile and injurious fighting becomes rare (i.e. in species in which  
294  $D_{SI}$  is functionally linked to weapon use). When  $D:D_{SI}$  is high on the other hand, the cost of  
295 self-inflicted damage will be lower than the benefit gained from damaging an opponent, and  
296 injurious fighting may spread. Furthermore, under the Hawk-Dove model, the benefit of

297 using a non-injurious display (dove) or fighting injuriously (hawk) is frequency-dependent,  
298 that is the best strategy depends on what an individual's opponent chooses to do. This  
299 stems from the fact that under the Hawk-Dove model, C results only from the opponent's  
300 actions. However, if significant  $D_{SI}$  is present then C is no longer the result of the opponent's  
301 actions but of the individual's own actions as well and as such  $D_{SI}$  may have significant  
302 implications for the frequency-dependent predictions of the Hawk-Dove model.

303

#### 304 *Future research*

305 Here we have discussed how self-inflicted damage is possible during contests that involve  
306 injurious fighting. Indeed, although understudied, self-injurious fighting occurs in examples  
307 from diverse animal taxa and may therefore represent a general constraint under which  
308 aggressive behaviour evolves. The true implications of  $D_{SI}$  can only be uncovered with  
309 focussed theoretical and empirical research. Theoretical studies modelling the evolution of  
310 fighting with the inclusion of  $D_{SI}$  will be necessary to shed light on just how  $D_{SI}$  may impact  
311 the evolution of non-injurious displays versus injurious fighting. Theoretical models could  
312 also be used to understand what determines the  $D:D_{SI}$  threshold at which inflicting damage  
313 on an opponent is no longer worthwhile, e.g. the value the competitors place on the  
314 contested resource. Furthermore, while it is clear that damage and  $D_{SI}$  both come at a cost,  
315 how these costs compare remains unclear. For instance, is it more costly for a beetle to snap  
316 its horn or to be pierced by its opponent's horn? Is it more costly for an anemone to tear off  
317 pieces of its own acrorhagi or to be stung? Examining these costs empirically may help to  
318 resolve why injurious fighting persists in species in which  $D_{SI}$  is a common or even obligatory  
319 consequence of inflicting an attack (e.g. *A. equina*). Furthermore unravelling the costs of

320 damage and  $D_{SI}$  may be a relatively straightforward feat. For example, the damage state of  
321 individuals could be experimentally manipulated (e.g. cutting off sections of a beetle's horns)  
322 prior to staged agonistic encounters or observations of other behaviours that influence  
323 access to resources (in fact similar studies have previously been carried out to investigate  
324 the effect of leg autotomy on spider contest success, Johnson & Jakob, 1999; Taylor &  
325 Jackson, 2003). Indeed, the effects of damaged weapons could also be investigated with  
326 respect to longer-term life-history allocation. An alternative approach would be to simply  
327 allow individuals to fight and on identifying the attacker and recipient (or an individual  
328 classed as both in a fight involving mutual attacks), taking performance measures or fitness  
329 correlates from each individual. How the rate and power of attack affect these costs also  
330 warrants investigation and could again be manipulated. Finally, a further area of interest  
331 would be to investigate if and how individuals cope with experiencing  $D_{SI}$ . When their  
332 weapons are out of action, do individuals switch tactics within a fight or sit out the fight  
333 entirely? For example, when the impact of shell rapping was experimentally dampened in  
334 the hermit crab *Pagurus bernhardus*, individuals increased their use of an alternate agonistic  
335 behaviour, rocking, to improve their chances of evicting their opponent (Edmonds & Briffa,  
336 2016). Perhaps more skilful individuals are better able cope with  $D_{SI}$  as well as being better  
337 able to prevent it?

338 Overall the message of our paper is simple; damage costs during animal contests can  
339 result not just from the agonistic action of one's opponent but also as a result of one's own  
340 agonistic action. Just how this self-inflicted damage affects contest dynamics and the  
341 evolution of fighting warrants the advent of new research in the field of animal contests.

342



343 **References**

344 Banks, W. J., Epling, G. P., Kainer, R. A., & Davis, R. W. (1968) Antler growth and  
345 osteoporosis I. Morphological and morphometric changes in the costal compacta during the  
346 antler growth cycle. *The Anatomical Record*, *162*, 387-397. (doi: 10.1002/ar.1091620401)

347

348 Bartosz , G., Finkelshtein, A., Przygodzki, T., Bsor, T., Nesher, N., Sher, D., & Zlotkin, E. (2008)  
349 A pharmacological solution for a conspecific conflict: ROS-mediated territorial aggression in  
350 sea anemones. *Toxicon*, *51*, 1038-1050. (doi: 10.1016/j.toxicon.2008.01.017)

351

352 Batchelor, T. P. & Briffa, M. (2010) Influences on resource-holding potential during  
353 dangerous group contests between wood ants. *Animal Behaviour*, *80*, 443-449. (doi:  
354 10.1016/j.anbehav.2010.05.030)

355

356 Batchelor, T. P. & Briffa, M. (2011) Fight tactics in wood ants: individuals in smaller groups  
357 fight harder but die faster. *Proceedings of the Royal Society B: Biological Sciences*, *278*,  
358 3243-3250. (doi:10.1098/rspb.2011.0062)

359

360 Batchelor, T. P., Santini, G., & Briffa M. (2012) Size distribution and battles in wood ants:  
361 group resource-holding potential is the sum of the individual parts. *Animal Behaviour*, *83*,  
362 111-117. (doi: 10.1016/j.anbehav.2011.10.014)

363

364 Bigger, C. H. (1980) Interspecific and intraspecific acrorhagial aggressive behaviour among  
365 sea anemones: A recognition of self and not-self. *Biological Bulletin*, 159, 117-134.

366

367 Bigger, C. H. (1982) The cellular basis of the aggressive acrorhagial response in of sea  
368 anemones. *Journal of Morphology*, 173, 259-278. (doi: 10.1002/jmor.1051730303)

369

370 Bonnin, J. P. (1964) Recherches sur la 'réaction d'agression', et sur la fonctionnement des  
371 acrorhages d'*Actinia equina* L. *Bulletin Biologique de la France et de la Belgique*, 98, 225-250.

372

373 Brace, R. C., Pavey, J., & Quickie, D. L. J. (1979) Intraspecific aggression in the colour morphs  
374 of the anemone *Actinia equina*: the 'convention' governing dominance ranking. *Animal*  
375 *Behaviour*, 27, 553-561. (doi: 10.1016/0003-3472(79)90190-8)

376

377 Briffa, M. & Elwood, R. W. (2009) Difficulties remain in distinguishing between mutual and  
378 self-assessment in animal contests. *Animal Behaviour*, 77, 759-762. (doi:  
379 10.1016/j.anbehav.2008.11.010)

380

381 Clutton-Brock, T. H. (1982) The functions of antlers. *Behaviour*, 79, 108-124. (doi:  
382 10.1163/156853982X00201)

383

384 Crisco, J. J., Fiore, R., Beckwith, J. G., Chu, J. J., Gunnar Brolinson, P., Duma, S., McAllister, T.  
385 W., Duhaime, A-C., & Greenwood, R. M. (2010) Frequency and location of head impact  
386 exposures in individual collegiate football players. *Journal of Athletic Training*, 45(6), 549-  
387 559.

388

389 Davidson D.W., Kamariah A.S., & Billen J. (2011) Histology of structures used in territorial  
390 combat by Borneo's 'exploding ants'. *Acta Zoologica – Stockholm*, 93, 487-491. (doi:  
391 10.1111/j.1463-6395.2011.00523.x)

392

393 Davidson D.W., Lessard J.P., Bernau C.R., & Cook S.C. (2007) The tropical ant mosaic in a  
394 primary Bornean rain forest. *Biotropica*, 39, 468-475 (doi: 10.1111/j.1744-  
395 7429.2007.00304.x)

396

397 Edmonds, E. & Briffa, M. (2016) Weak rappers rock more: hermit crabs assess their own  
398 agonistic behaviour. *Biology Letters*, 12: 20150884. (doi: 10.1098/rsbl.2015.0884)

399

400 Goubault, M., Batchelor, T. P., Linforth, R. S. T., Taylor, A. J., & Hardy, I. C. W. (2006) Volatile  
401 emission by contest losers revealed by real-time chemical analysis. *Proceedings of the Royal*  
402 *Society B*, 273, 2853-2859. (doi: 10.1098/rspb.2006.3655)

403

404 Goubault, M., Batchelor, T. P., Romani, R., Linforth, R. S. T., Fritzsche, M., Francke, W., &  
405 Hardy, I. C. W. (2008) Volatile chemical release by bethylid wasps: identity, phylogeny,  
406 anatomy and behaviour. *Biological Journal of the Linnean Society*, *94*, 837-852.

407

408 Green, C. M., Petrou, M. J., Fogarty-Hover, M. L. S., & Rolf, C. G. (2007) Injuries among  
409 judokas during competition. *Scandinavian Journal of Medicine and Science in Sports*, *17*, 20-  
410 210. (doi: 10.1111/j.1600-0838.2006.00552.x)

411

412 Guskiewicz, K. M., McCrea, M., Marshall, S. W., Cantu, R. C., Randolph, C., Barr, W., Onate, J.  
413 A., & Kelly, J. P. (2003) Cumulative effects associated with recurrent concussion in collegiate  
414 football players. *JAMA*, *290*, 2549-2555.

415

416 Guskiewicz, K. M., Marhsall, S. M., Bailes, J., McCrea, M., Cantu, R. C., Randolph, C., & Jordan,  
417 B. D. (2005) Association between recurrent concussion and late-liflife cognitive impairment in  
418 retired professional football players. *Neurosurgery*, *57* (4), 719-726.

419

420 Hurst, A. (1917) Gas-poisoning. In *Medical diseases of the war*, 308-317. London, UK:  
421 Edward Arnold.

422

423 Johnson, H. E., Bleich, V. C., Krausman, P. R., & Koprowski, J. L. (2007) Effects of antler  
424 breakage on mating behaviour in male tule elk (*Cervus elaphus nannodes*). *European Journal*  
425 *of Wildlife Research*, 53, 9-15. (doi: 10.1007/s10344-006-0060-4)

426

427 Johnson, S. A., & Jakob, E. M. (1999) Leg autotomy in a spider has minimal costs in  
428 competitive ability and development. *Animal Behaviour*, 57, 957-965.

429

430 McCullough, E. L. (2014) Mechanical limits to maximum weapon size in a giant rhinoceros  
431 beetle. *Proceeding of the Royal Society B: Biological Sciences*, 281: 20140696. (doi:  
432 10.1098/rspb.2014.0696)

433

434 McCullough, E. L. & Emlen, D. J. (2013) Evaluating the costs of a sexually selected weapon:  
435 big horns at a small price. *Animal Behaviour*, 86, 977-985. (doi:  
436 10.1016/j.anbehav.2013.08.017)

437

438 McCullough, E. L. & Tobalske, B. W. (2013) Elaborate horns in a giant rhinoceros beetle incur  
439 negligible aerodynamic costs. *Proceedings of the Royal Society B: Biological Sciences*, 280,  
440 20130197. (doi: 10.1098/rspb.2013.0197)

441

442 Murray, M. G. (1987) The closed environment of the fig receptacle and its influence on male  
443 conflicts in the Old World fig wasp, *Philotrypesis pilosa*. *Animal Behaviour*, 38, 186-193.

444

445 Nüchter, T., Benoit, M., Engel, U., Ozbek, S., & Holstein, W. (2006) Nanosecond-scale  
446 kinetics of nematocyst discharge. *Current Biology*, 16, R316-R318. (doi:  
447 10.1016/j.cub.2006.03.089)

448

449 Palaoro, A.V. & Briffa, M. (2016) Weaponry and defenses in fighting animals: how allometry  
450 can alter predictions from contest theory. *Behavioural Ecology*.

451

452 Parker, G. A. & Rubenstein, D. I. (1981) Role assessment, reserve strategy, and acquisition of  
453 information in asymmetric animal conflicts. *Animal Behaviour*, 29, 221-240.

454

455 Patek, S. N., Korff, W. L., & Caldwell, R. L. (2004) Deadly strike mechanism of a mantis  
456 shrimp. *Nature*, 428, 819-820. (doi:10.1038/428819a)

457

458 Payne, R. J. H. (1998) Gradually escalating fights and displays: the cumulative assessment  
459 model. *Animal Behaviour*, 56, 651-662. (doi:10.1006/anbe.1998.0835)

460

461 Rudin, F. S. & Briffa, M. (2011) The logical polyp assessments and decisions during contests  
462 in the beadlet sea anemone *Actinia equina*. *Behavioural Ecology*, 22, 1278-1285. (doi:  
463 10.1093/beheco/arr125)

464

465 Ryan, A. J. (1987) Intracranial injuries resulting from boxing: A review (1918-1985). *Clinics in*  
466 *Sports Medicine*, 6, 31-40.

467

468 Ryan, A. J. (1991) Protecting the sportsman's brain (concussion in sport). Annual guest  
469 lecture 1990, London Sports Medicine Institute. *British Journal of Sports Medicine*, 25, 81-86.

470

471 Shackleton, K., Al Toufalia, H., Balfour, N. J., Nascimento, F. S., Alves, D. A., & Ratnieks, F. L.  
472 W. (2015) Appetite for self-destruction: suicidal biting as a nest defence strategy in a  
473 *Trigona* stingless bees. *Behavioural Ecology and Sociobiology*, 69, 273-281. (doi:  
474 10.1007/s00265-014-1840-6)

475

476 Shorter, J. R. & Rueppell, O. (2015) A review on self-destructive defense behaviours in social  
477 insects. *Insectes Sociaux*, 59, 1-10. (doi: 10.1007/s00040-011-0210-x)

478

479 Šobotník, J., Bourguignon, T., Hanus, R., Demianová, Z., Pytelková, J., Mareš, M., Foltynová,  
480 P., Preisler, J., Cvačka, Krasulová, J., & Roisin, Y. (2012) Explosive backpacks in old termite  
481 workers. *Science*, 337, 436. (doi: 10.1126/science.1219129)

482

483 Stabili, L., Schirosi, R., Parisi, M. G., Piraino, S., & Cammarata, M. (2015) The mucus of  
484 *Actinia equina* (Anthozoa, Cnidaria): An unexplored resource for potential applicative  
485 purposes. *Marine Drugs*, 13, 5276-5296. (doi: 10.3390/md13085276)

486

487 Swartz, E. E., Broglio, S. P., Cook, S. B., Cantu, R. C., Ferrara, M. S., Guskiewicz, K. M., &  
488 Myers, J. L. (2015) Early results of a helmetless-tackling intervention to decrease head  
489 impacts in football players. *Journal of Athletic Training*. 50(12), 1219-1222.

490

491 Szinicz, L. (2005) History of chemical and biological weapons. *Toxicology*, 214, 167-181. (doi:  
492 10.1016/j.tox.2005.06.011)

493

494 Taylor, P. W., & Jackson, R. R. (2003) Interacting effects of size and prior injury in jumping  
495 spider conflicts. *Animal Behaviour*, 65, 787-794. (doi: 10.1006/anbe.2003.2104)

496



497 Uematsu, K., Kutsukake, M., Fukatsu, T., Shimada, M., & Shibao, H. (2007) Altruistic  
498 defenders in a Japanese gall-forming aphid, *Quadrartus yoshinomiya* (Homoptera:  
499 Aphididae: Hormaphidinae). *Sociobiology*, *50*, 711-724.

500

501 Uematsu, K., Kutsukake, M., Fukatsu, T., Shimada, M., & Shibao, H. (2010) Altruistic colony  
502 defence by menopausal female insects. *Current Biology*, *20*, 1182-1186.

503

504 Varnon, J., Courtney, M., & Ekis, T. R. (1995) Self-wounding of assailants during stabbing and  
505 cutting attacks. *SWAFS Journal*, *17*(1), 19.

506

507 Wilde, G. J. S. (1998) Risk homeostasis theory: an overview. *Injury Prevention*, *4*, 89-91.

508

509 Wilkinson, P. F. & Shank, C. C. (1976) Rutting-fight mortality among musk oxen on Banks  
510 Island, Northwest Territories, Canada. *Animal Behaviour*, *24*, 756-758. (doi: 10.1016/S0003-  
511 3472(76)80004-8)

512

513 Williams, R. B., LeMagnen, J., & MacLeod, P. (1978) Some recent observations on the  
514 acrorhagi of sea anemones. *Journal of the Marine Biological Association of the United*  
515 *Kingdom*, *58*, 787-788.

516

517

518

519

520

521

522

523

524

525

526

**Table 1** Examples of self-inflicted damage via attacks in human and non-human animals

Group	Species	Context	Weapon(s)	Self-inflicted damage via attack	Likelihood	Severity	Reversibility	Source
<b>Anthozoa</b>	Beadlet sea anemone <i>Actinia equina</i>	Dyadic contests	Specialised stinging tentacles (acrorhagi)	Loss of acrorhagial ectoderm	Certain	Low to high	~7 days	Bonnin, 1964; Bigger, 1980
<b>Crustacea</b>	Peacock mantis shrimp <i>Odontodactylus scyllarus</i>	Predation	Dactyl club	Pitting and damage of dactyl heel over time	Certain (over multiple fights)	Mild	Replaced every few months	Patek et al., 2004
<b>Insecta</b>	Asian rhinoceros beetle <i>Trypoxylus dichotomus</i>	Dyadic contests	Long, forked head horn	Horn breakage	Increases with horn size	Low to high	Irreversible	McCullough, 2014
	Termite <i>Neocapritermes taracua</i>	Colony defence	"Explosive backpacks" (autothysis)	Death via autothysis	Certain	Very high	Irreversible	Šobotník et al., 2012
	Stingless bees <i>Trigona hyalinata</i>	Nest defence	Biting	Death (individuals stick to intruder)	High to certain	Very high	Irreversible	Shackleton et al. 2015
	Carpenter Ant <i>Camponotus cylindricus</i>	Colony defence and dyadic contests	Biting, secretion of adhesive corrosive substance	Death (individuals stick to intruder)	Certain	Very High	Irreversible	Davidson et al. 2007; 2011
	Gall-forming aphid <i>Quadartus yoshinomyiai</i>	Colony defence	Secretion of adhesive waxy substance	Death (individuals stick to intruder)	Certain	Very High	Irreversible	Uematsu et al., 2007; 2010
<b>Mammalia</b>	Cervids (general)	Rutting (dyadic contests)	Antlers	Antler breakage	<25% males	Low to high	Seasonal	Clutton-Brock, 1982
	Tule Elk <i>Cervus elaphus nannodes</i>	Rutting (dyadic contests)	Antlers	Antler breakage	>80% males	Low to high	Seasonal	Johnson et al., 2007
	Humans <i>Homo sapiens sapiens</i>	Boxing	Hands (punching)	"boxer's fracture" - breakage of metacarpal bones from impact with skull	Certain	High	6-8 weeks	Ryan, 1987; 1991

American football	Head	Concussion, brain and spinal trauma, cognitive impairment depending on severity and recurrence	Highly likely (~1000 head impacts per season)	Mid to high	Dependent on severity	Guskiewicz et al., 2003; 2005; Swartz et al., 2015
Judo	Upper body (throwing)	Sprain / fracture depending on severity	Likely (~13.5%)	Low to high	~ 25 days	Green et al., 2007
War (WWI)	Chlorine gas (first use by German soldiers)	Respiratory irritation to pulmonary edema	Highly likely	Very high	~5% death rate	Hurst, 1917; Szinicz, 2005
Stabbing attacks	Knife	Lacerations and stab wounds	Highly likely	Low to high	Dependent on severity	Varnon et al., 1995

527

528

529

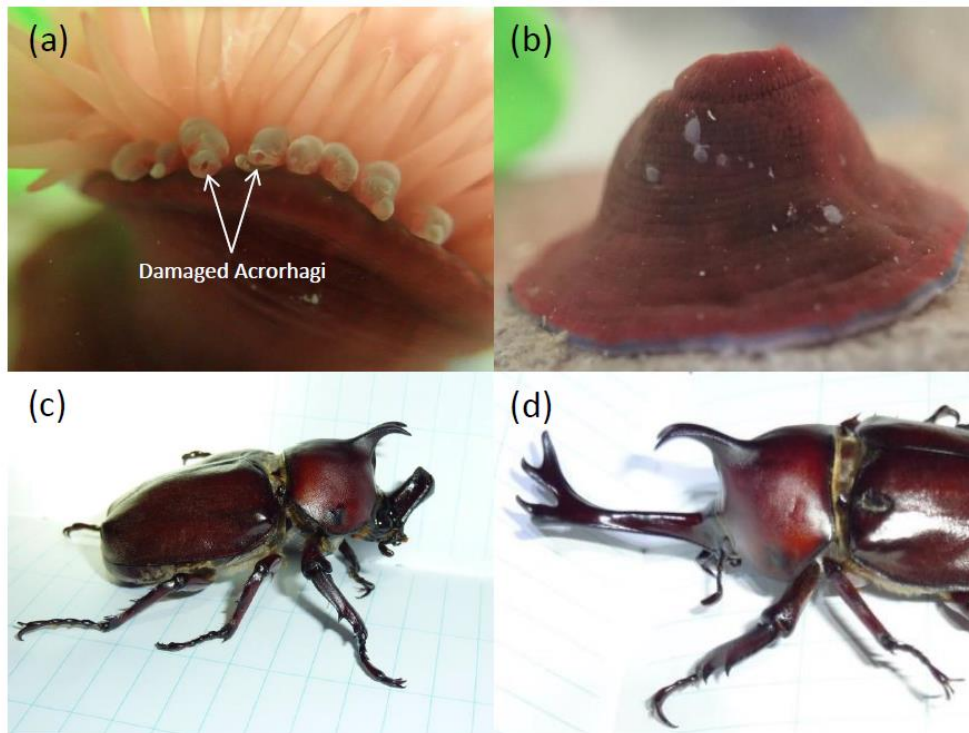
530

531

532

533

534



535

536 **Figure 1** Examples of damage to attacker and receiver (a) A beadlet sea anemone *Actinia*  
537 *equina* exhibits holes in its acrorhagi as a result of inflicting an attack on (b) Acrorhagial  
538 peels can be seen on the body column of the recipient of attack (Anemone pictures: Sarah  
539 M. Lane) (c) A male Asian rhinoceros beetle *Trypoxylus dichotomus* with a broken head horn  
540 resulting from a fight with another male. (d) A male with punctured elytra, caused by the  
541 sharp tines seen on the thoracic horn (Beetle pictures: Erin L. McCullough).

542