1 **THE PRICE OF ATTACK: RETHINKING DAMAGE COSTS IN ANIMAL CONTESTS**

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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

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　　　　　　　　　　　$C \text{ } accumulated = E + D$　　　　　　　　　　(1)

49　Giving up is triggered when: -

50　　　　　　　　　　　$C \text{ } accumulated > C_{max}$　　　　　　　　　　(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　　　　　　　　　　　$C \text{ } accumulated = E + D + D_{SI}$　　　　　　　　(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, Bsor, Nesher, 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, Toufailia, Balfour, Nascimento, Alves &

187   Ratnieks,2015). Similarly carpenter ant *Camponotus (Colobopsis) cylindricus* and gall-

188   forming aphid *Quadrartus yoshinomiyai* 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

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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
Anthozoa	Beadlet sea anemone *Actinia equina*	Dyadic contests	Specialised stinging tentacles (acrorhagi)	Loss of acrorhagial ectoderm	Certain	Low to high	~7 days	Bonnin, 1964; Bigger, 1980
Crustacea	Peacock mantis shrimp *Odontodactylus scyllarus*	Predation	Dactyl club	Pitting and damage of dactyl heel over time	Certain (over multiple fights)	Mild	Replaced every few months	Patek et al., 2004
Insecta	Asian rhinocerus beetle *Trypoxylus dichotomus*	Dyadic contests	Long, forked head horn	Horn breakage	Increases with horn size	Low to high	Irreversible	McCullough, 2014
	Termite *Neocapritermes taracua*	Colony defence	"Explosive backpacks" (autothysis)	Death via autothysis	Certain	Very high	Irreversible	Šobotník et al., 2012
	Stingless bees *Trigona hyalinata*	Nest defence	Biting	Death (individuals stick to intruder)	High to certain	Very high	Irreversible	Shackleton et al. 2015
	Carpenter Ant *Camponotus (Colobopsis) cylindricus*	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 *Quadrartus yoshinomiyai*	Colony defence	Secretion of adhesive waxy substance	Death (individuals stick to intruder)	Certain	Very High	Irreversible	Uematsu et al., 2007; 2010
Mammalia	Cervids (general)	Rutting (dyadic contests)	Antlers	Antler breakage	<25% males	Low to high	Seasonal	Clutton-Brock, 1982
	Tule Elk *Cervus elaphus nannodes*	Rutting (dyadic contests)	Antlers	Antler breakage	>80% males	Low to high	Seasonal	Johnson et al., 2007
	Humans *Homo sapiens sapiens*	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

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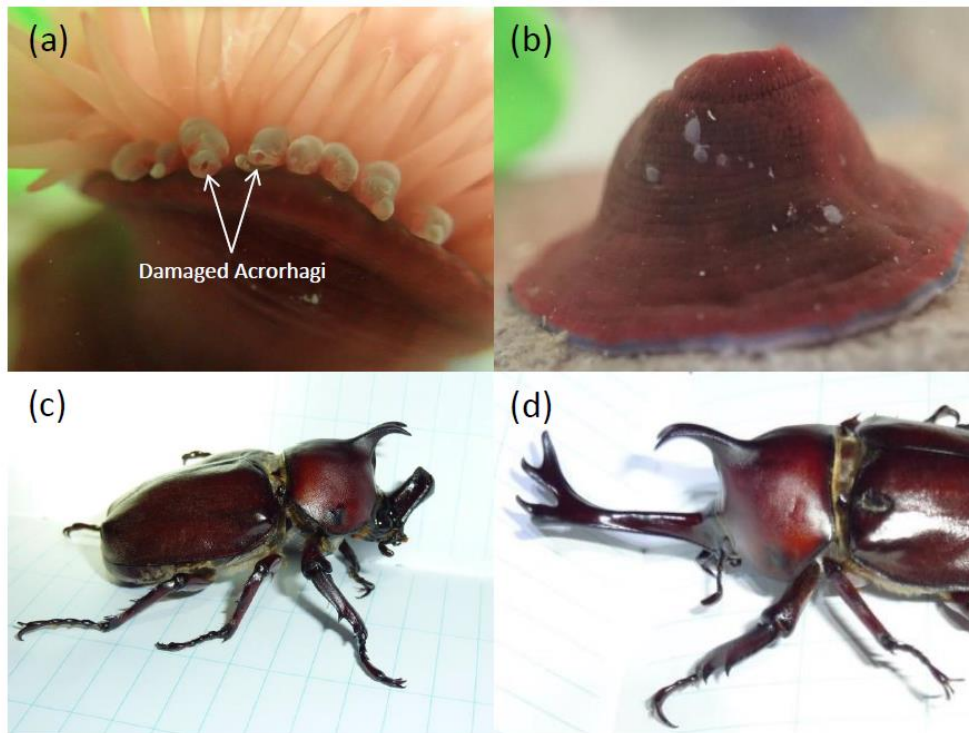
Figure 1 Examples of damage to attacker and receiver (a) A beadlet sea anemone *Actinia equina* exhibits holes in its acrorhagi as a result of inflicting an attack on (b) Acrorhagial peels can be seen on the body column of the recipient of attack (Anemone pictures: Sarah M. Lane) (c) A male Asian rhinoceros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

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