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THE PRICE OF ATTACK: RETHINKING DAMAGE COSTS IN ANIMAL CONTESTS

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

Keywords: animal contests; cumulative assessment model; damage costs; injurious contests; 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)

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

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

Giving up is triggered when: -

$$C_{\text{accumulated}} > C_{\max} \quad (2)$$

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

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

$$C_{\text{accumulated}} = E + D + D_{SI} \quad (3)$$

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

EVIDENCE OF SELF-INFLICTED DAMAGE VIA ATTACKS IN NONHUMAN ANIMALS

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

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

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

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, Bsoir, 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

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

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

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

Self-inflicted damage during colony defence: social insects

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

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

EVIDENCE OF SELF-INFLICTED DAMAGE VIA ATTACKS IN HUMANS

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

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

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

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

IMPLICATIONS FOR ANIMAL CONTEST THEORY AND ANALYSIS

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

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

Future research

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

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

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

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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 <i>Actinia equina</i>	Dyadic contests	Specialised stinging tentacles (acrorhagi)	Loss of acrorhagial ectoderm	Certain	Low to high	~7 days	Bonnin, 1964; Bigger, 1980
Crustacea	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
Insecta	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>Quadrtus yoshinomiya</i>	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 <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

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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).