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 ($C_{\text{max}}$). Under this model, an individual gives up when the accumulated costs of persisting exceed this threshold. CAM predicts that the velocity with which $C_{\text{max}}$ 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
Before the introduction of gloves around 1897, there were no recorded deaths in professional boxing. This is because a human hand will break on impact with a human skull long before the skull does. Thanks to boxing gloves, “boxer’s fracture” (the breakage of the metacarpal bones on impact with an immovable object) is now restricted to emergency department waiting rooms after brawls in bars, whilst 3 to 4 professional fights end in a death every year in the USA alone and 15% of professional fighters suffer permanent brain injury during their career (Ryan, 1987; 1991). Gloves have thus enabled boxers to inflict injury whilst avoiding the self-inflicted injuries that would otherwise accrue from punching an opponent.

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

\[ C_{\text{accumulated}} = E + D \]  

(1)

Giving up is triggered when:

\[ C_{\text{accumulated}} > C_{\text{max}} \]  

(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 $C_{\text{max}}$. 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.

\[ C_{\text{accumulated}} = E + D + D_{SI} \]  

(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 infliectors 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 DSI 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, DSI during an attack is a risk but not a certainty. Severity is the loss of fitness resulting from (a) loss of function due to DSI 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 DSI.

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
Thus far the most well-described and extreme example of self-inflicted damage to attackers is found in contests between beadlet sea anemones *Actinia equina*. *A. equina* are among the simplest animals to engage in contests. They lack a centralised nervous system but possess weapons in the form of specialised stinging tentacles called acrorhagi which contain high concentrations of stinging nematocytes and are used solely for fighting other anemones (Williams, 1978; Brace, Pavey, & Quickie, 1979; Bigger, 1982). During contests, anemones scrape inflated acrorhagi along their opponent’s body column. Pieces of the attacker’s nematocyte-filled acrorhagial ectoderm (known as “peels”) stick to the recipient of the attack causing localised necroses (Nüchter, Benoit, Engel, Ozbek, & Holstein, 2006; Bartosz, Finkelshtein, Przygodzki, Bsor, Nesher, Sher, & Zlotkin, 2008) whilst the attacking anemone is left with holes in its acrorhagi (figure 1). The greater the number of peels landed, the more damage done to the recipient and the greater chance of winning for the attacker (Rudin & Briffa, 2011). However in *A. equina*, individuals are unable to damage their opponents without also damaging themselves, and an increase in peels means an increase in damage to the attacker by necessity. Furthermore, while healing appears to be relatively rapid (< 7 days – SML personal observation) the accumulated costs of damage are unlikely to be immaterial, especially in fights in which both individuals receive and inflict attacks. Thus in *A. equina* the velocity at which $C_{max}$ is reached will be reliant upon the energetic costs of remaining in the contest, the number of peels received and the number of peels inflicted. The relative costs of receiving and inflicting peels may of course not be identical, in which case the two kinds of damage costs may make different contributions to $C_{max}$. For instance, the physical damage caused by receiving and inflicting peels presumably leaves individuals at greater risk of infection from pathogens until healing is complete (although 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 DSI 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, Toufailia, Balfour, Nascimento, Alves & Ratnieks, 2015). Similarly carpenter ant *Camponotus* (*Colobopsis*) *cylindricus* and gall-forming aphid *Quadrartus yoshinomiyai* 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 & Ruepell, 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 *Dsi* 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).
Thus, although individuals with larger horns may be able to elicit more damage in a single attack, individuals with smaller horns are able to inflict damage for longer before damaging themselves. Furthermore, some individuals may be able to inflict more damage without hurting themselves not due to morphological differences, but rather differences in skill, being better able to land an attack without injuring themselves. Skilful individuals may also be better able to successfully land a single blow, securing a victory without having to strike repeatedly, a skill which would be of particular importance in situations where $D_{SI}$ increases with attack rate. Individuals who possess a high $D:D_{SI}$ ratio (e.g. 6:1) will be able to inflict a greater amount of damage to their opponent before reaching their maximum cost threshold ($C_{max}$) and thus be more likely to win contests in which victory relies upon attack rate and/or power.

The $D:D_{SI}$ differential will likely vary across as well as within species. In species in which the risk of $D_{SI}$ is very low, the ability to damage an opponent may be very important in comparison to species in which the risk of $D_{SI}$ is high. Of course, the rate at which $C_{max}$ is reached will still be dependent upon damage costs inflicted on individuals by their opponent and thus the $D:D_{SI}$ ratio of an individual’s opponent will also affect the velocity with which $C_{max}$ is reached and therefore who gives up first. In species with a low risk of $D_{SI}$ (and in contests between opponents with disparate $D:D_{SI}$ ratios), contest duration will be negatively correlated with winner RHP (resource holding potential). The higher winner RHP, the more injuries the winner will be able to inflict on its opponent before reaching its own $C_{max}$ and the quicker its opponent will be to retreat (leading to problems distinguishing between mutual and self-assessment as discussed by Briffa & Elwood, 2009; see also Palaoro and Briffa 2016 for a consideration of how the allometric growth of weapons and defences may
complicate our ability to distinguish between mutual- and self-assessment). But if damage inflicted and $D_{SI}$ are very closely linked, then damage inflicted in a fight may become less relevant for fight outcome and the link between absolute RHP and contest duration less clear. Furthermore in species in which the risk of $D_{SI}$ is high, contests may be over faster than in species with a lower $D_{SI}$ risk, especially in contests with mutual attacks, in which the costs of self-inflicted damage are combined with the costs of receiving damage, pushing individuals faster towards their $C_{max}$.

To this day, many empirical studies of contest behaviour base their questions and predictions on the classic Hawk-Dove model of John Maynard Smith and Geoff Parker (1976). This model assumes that the evolution and prevalence of restraint (non-injurious fighting) is due to negative frequency dependent selection acting on fighting strategies and the cost of injurious fighting ($C$) usually far outweighing the value of the contested resource. Under the Hawk-Dove model, the only cost of fighting is that of receiving injuries from the actions of an opponent, but what happens when we factor in the additional cost of inflicting injuries?

Perhaps the most obvious consequence of incorporating $D_{SI}$ into the Hawk-Dove model is that it increases $C$, making the evolution of injurious fighting even less likely. However, the extent to which $D_{SI}$ contributes to $C$ will depend on the damage to $D_{SI}$ ratio. When damage and $D_{SI}$ are very closely linked (e.g. 1:1), the cost of self-inflicted damage will (at some threshold ratio) outweigh the benefits of damaging an opponent, such that inflicting damage is no longer worthwhile and injurious fighting becomes rare (i.e. in species in which $D_{SI}$ is functionally linked to weapon use). When $D:D_{SI}$ is high on the other hand, the cost of self-inflicted damage will be lower than the benefit gained from damaging an opponent, and 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 DSI 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 DSI 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 DSI can only be uncovered with focussed theoretical and empirical research. Theoretical studies modelling the evolution of fighting with the inclusion of DSI will be necessary to shed light on just how DSI may impact the evolution of non-injurious displays versus injurious fighting. Theoretical models could also be used to understand what determines the D:DSI 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 DSI 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 DSI 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.
References


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<tr>
<td>Stabbing attacks</td>
<td>Knife</td>
<td>Lacerations and stab wounds</td>
<td>Highly likely</td>
<td>Low to high</td>
<td>Dependent on severity</td>
<td>Varnon et al., 1995</td>
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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).