Essay

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 accumulated not only 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 to fully understand what drives an individual to make the decision to give up, and we call for further research into this area.
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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, while three to four professional fights end in a death every year in the U.S.A. alone and 15% of professional fighters suffer permanent brain injury during their career (Ryan, 1987, 1991). Gloves have thus enabled boxers to inflict injury while 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 that 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) (Payne, 1998). The higher the accumulated costs, the sooner C_{max} will be reached and the sooner the loser will retreat.

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

Giving up is triggered when

$$C \text{ accumulated} > C_{max} \tag{2}$$

CAM assumes that an individual's contest decisions are based upon self-assessment but recognizes 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 the potential self-inflicted damage costs of carrying out agonistic behaviour into account. In fact, to our knowledge, self-inflicted damage has so far not been considered as a cost of fighting in the 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.

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Thus, in situations in which 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.

$$C \text{ accumulated} = E + D + D_{SI} \qquad (3)$$

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 in which self-inflicted damage is absent. Under the predictions of the CAM, Payne (1998) argued 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 the 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, Parker and Rubenstein (1981) assumed 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 when it is only winners that perform the injurious behaviours.

EVIDENCE OF SELF-INFLICTED DAMAGE: NONHUMAN ANIMALS

Evidence of self-inflicted damage in attackers is limited, probably in part because, 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 noninjurious 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 (1) loss of function due to D_{SI} from the time of attack until healing is complete and (2) 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 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 *A. equina* anemones, which are among the simplest animals to engage in contests. They lack a centralized nervous system but possess weapons in the form of specialized stinging tentacles called acrorhagi which contain high concentrations of stinging nematocytes and are used solely for fighting other anemones (Bigger, 1982; Brace, Pavey, & Quickie, 1979; Williams, 1978). 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 localized necrosis (Bartosz et al., 2008; Nüchter, Benoit, Engel, Ozbek, & Holstein, 2006) while the attacking anemone is left with holes in its acrorhagi (Fig. 1). The greater the number of peels landed, the more damage is done to the recipient and the greater the 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, S.M. Lane, 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 not be identical, of course, 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 deer and beetles. 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 relatively low cost of beetle horns (McCullough & Emlen, 2013; McCullough & Tobalske, 2013), but both weapons run the risk of breakage during a contest (Fig. 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 ca. 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, *Dama dama*, 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