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The prevalence of weapon damage: a proportional meta-analysis

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Abstract

Sexually selected weapons are tools that are used in physical fights over mating opportunities. Individuals can face dire fitness consequences if they break their weapon and can no longer fight effectively; however, the costs and consequences of weapon damage have largely been ignored. In this study, the literature was systematically searched to examine the prevalence of weapon damage, and a phylogenetically controlled proportional meta-analysis was conducted to explore factors influencing the patterns of weapon damage across the animal kingdom. A total of 36 suitable studies were identified across 74 species and 13 orders for a total of 82 effect sizes. We found that weapon damage is common across taxa, with an average rate of damage of 9.4% across all observations. We found strong evidence that regenerative ability influences the patterns of weapon damage, with species capable of weapon regeneration exhibiting high prevalence of weapon damage. Herein, we discuss additional factors that may affect the likelihood, costs and consequences of weapon damage, including weapon size, weapon allometry, fighting behaviour and when and to what degree a species can regenerate its weapon. We argue that the risk of weapon damage is an important but underappreciated cost that could affect strategic fighting decisions, providing new insights into the role of weapon damage on the evolution of weapon morphology and contest behaviour within and among species.

The need to fight for access to mates or resources that attract mates, has led to the evolution of some of the most exaggerated and diverse traits in the animal kingdom, sexually selected weapons (Emlen, 2008; McCullough et al., 2016; Rico-Guevara & Hurme, 2019). Given their extreme and hypervariable size, most research on sexually selected weapons has focused on the costs of producing and bearing them, including developmental trade-offs (Emlen, 2001; Simmons & Emlen, 2006), impaired locomotion (Cummings et al., 2018; Fuchikawa & Okada, 2013; Goyens et al., 2015; Madewell & Moczek, 2006) and energetic costs (Allen & Levinton, 2007; Moen et al., 1999; Somjee et al., 2018; Tullis & Straube, 2017). In comparison, little attention has been devoted to the cost of using weapons during combat (McCullough, 2014; McEvoy et al., 2024) despite the importance of these costs for understanding the evolution of weapon morphology and fighting behaviour (Emberts et al., 2021; Lane & Briffa, 2017; Palaoro et al., 2020).

Weapons function as tools because they are used to physically displace and injure opponents during contests. Depending on a species' particular fighting style, weapons are used to push, grasp, pry, stab and/or strike opponents during trials of strength or all-out attacks (Palaoro & Peixoto, 2022). Therefore, weapons can experience remarkable mechanical loads when they are bent, twisted or compressed during a fight. Although weapons are structurally adapted to withstand these fighting loads (Kitchener, 1991; McCullough et al., 2014), they are not indestructible, and can break under natural conditions.

Weapon damage can have catastrophic fitness consequences, but the cost of damage appears to vary substantially across taxa. For example, in the Asian rhinoceros beetle, *Trypoxylus dichotomus*, males cannot repair or replace a broken horn, and males with broken horns are unable to fight for access to breeding territories (McCullough, 2014). Consequently, breaking a horn effectively removes the damaged male from the mating pool. By contrast, in tule elk, *Cervus elaphus nannodes*, antlers are shed and regrown every year, and broken antlers have no effect on a male's fighting or

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harem-holding success (Johnson et al., 2007). However, basic information on the rates of weapon damage, factors that contribute to variation in damage within and among species and the fitness ramifications of such damage is fundamentally lacking.

This study aims to provide a comprehensive understanding of the prevalence, costs and consequences of weapon damage across the animal kingdom. First, we systematically search the literature to collect reported rates of weapon damage and conduct a phylogenetically controlled proportional meta-analysis to test the following four factors that might explain the differences in weapon damage among taxa: regenerative capacity, weapon size, fighting behaviour and weapon allometry. Second, we discuss the underlying reason why these factors may influence the likelihood and costs of weapon damage. Finally, we explore the mechanism by which these factors may interact to influence the evolution of fighting behaviour, including the decision rules for initiating, escalating and abandoning a fight.

METHODS

Articles relevant to our meta-analysis were identified using several approaches. First, the online databases *Scopus* and *Web of Science* were searched using the following search terms: (‘animal fight*’ OR ‘male−male competit*’ OR ‘intrasexual combat’ OR ‘animal contest*’) AND (claw* OR antler* OR armament* OR horn* OR weapon* OR tusk* OR mandible*) AND (damage* OR injur* OR wound* OR pierc* OR break* OR broke*). The literature search was conducted on 17 April 2024 without filters or limitations using the ‘Topic’ search field in *Web of Science* and the ‘Article Title, Abstract, Keywords’ search field in *Scopus*. The search terms were based on the titles, abstracts and keywords of relevant publications already known to us. Second, additional empirical examples were identified through backward and forward searches of a recent review on intrasexually selected weapons by Rico-Guevara and Hurme (2019). The forward search was conducted on 9 May 2024 in *Scopus*. Third, studies recommended by reviewers and colleagues or that were cited by articles identified in our searches were also included. Despite our systematic and thorough literature search, some reports of weapon damage were likely missed because observations are often simply presented as a side note about the species' natural history or to explain why individuals were excluded from further analysis. Nevertheless, our data set represents an important first step in synthesizing the observed rates of weapon damage across diverse animal taxa.

Articles were included in our meta-analysis if they met the following inclusion criteria. First, the study must report damage of an intrasexually selected weapon, which is defined in this study as a structure that is used as a fighting tool during same-sex contests (*sensu* Rico-Guevara & Hurme, 2019). Therefore, shields and other combat traits that are not directly wielded during fights were excluded (Rico-Guevara & Hurme, 2019). Second, the study must report damage of the weapons themselves, which excluded estimates of other fighting injuries, such as body wounds or death. Estimates of missing or autotomized weapons were also excluded because whether weapon loss resulted from fighting was unclear. Third, the study must provide sufficient statistical information to calculate an effect size (i.e. the number of damaged individuals and total number of sampled individuals or the proportion of damaged individuals and total sample size). If these data were not directly reported, then the authors were contacted to obtain the missing information or raw data where possible. Finally, the study must be available in English. A summary of the literature screening process and full list of the included and excluded studies are presented in the supplementary material (Fig. S1 and Table S1) in accordance with the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (O'Dea et al., 2021).

A proportional meta-analysis was conducted to compare the prevalence of weapon damage across observations. Considering that the observed proportions were significantly skewed towards 0, we performed the Freeman−Tukey double arcsine transformation to normalize the variances (Barker et al., 2021; Wang, 2023) using the escalc function in the R package metafor (Viechtbauer, 2010). For plotting purposes, back transformations of the double arcsine proportions were conducted in accordance with the recommendations by Wang (2023).

All possible effect sizes were extracted from each study. Whenever possible, only the prevalence of serious weapon damage was reported (e.g. broken claw). The severity of weapon damage can vary substantially, and fitness ramifications will also vary accordingly. Scratches and other superficial damage are unlikely to have a major impact on the fighting ability of males, but the accumulation of minor injuries can result in catastrophic failure caused by fatigue (see Consequences of Weapon Damage for Fighting Behaviour below). However, at present, our ability to make conclusions about the fitness costs of weapon damage is impeded due to lack of information.

To control for potential nonindependence arising from the use of multiple effect sizes from the same study or species, study and species were included as random effects in our statistical analyses. To control for the nonindependence of effect sizes caused by shared evolutionary history, a supertree containing all 74 species in our data set was created using the Open Tree of Life (OTL) database (Hinchliff et al., 2015) and rotl package in R (Michonneau et al., 2016). For species not included in the latest synthetic tree (OTL version 14.9), a substitution was found in the OTL database from the same genus (three cases) or tribe (three cases). Species substitutions are reported in the supplementary material (Table S2). Branch lengths were initially set to 1 and then made ultrametric using Grafen's method in the R package *ape* (Paradis et al., 2004). The final tree (Fig. S2) was converted into a variance−covariance matrix for inclusion in the meta-analysis models.

Four moderators were included in our meta-analysis that might influence the prevalence of weapon damage. First, we categorized each species by their regenerative capacity (Yes/No), which we defined as the ability to regrow or replace a weapon. We predicted that the prevalence of weapon damage would be higher among species that can regenerate their weapons because damage is reversible and, therefore, less costly. Second, each species was classified into two main size categories based on their relative weapon size. ‘Large’ weapons are defined as being longer than one-third of the total length of the animal's body, and ‘small’ weapons are defined as being shorter than one-third the length of the body. Weapon and body sizes were based on measurements reported for the largest males in each species. We predicted that the prevalence of weapon damage would be higher among species with relatively large weapons because they will experience higher bending stresses during fights. Third, for species with published descriptions of fighting behaviour (i.e. Artiodactyla; Caro et al., 2003), we categorized whether the species used their weapons to ram an opponent with rapid and forceful blows (Yes/No). We predicted that rammers would have higher rates of damage because the risk of brittle fracture increases under rapid loading caused by the viscoelasticity of biomaterials (Wainwright et al., 1976). Finally, the allometric slope of the weapon was reported whenever the study reporting weapon damage also included an estimate of weapon allometry. For dimorphic species with large ‘major’ males and small ‘minor’ males, the allometric slope for minor males was reported. This is because weapon allometries are shallower in major males than in minor males in holometabolous insects, which is due to resource limitation during pupal development (Kochensparger et al., 2024). We predicted that weapons with steep allometries would have higher rates of damage because of their disproportionately large size. Allometric slope estimates were based on log-transformed data for all observations. Our complete data set, including the moderator variables, is available in Table S2.

Multilevel meta-regression models were fitted using the rma.mv function in the R package metafor (Viechtbauer, 2010). To determine the overall effect size of the data set, a multilevel random-effects model was run with study, species, phylogeny (using the variance–covariance matrix described previously) and observation ID as random effects (Nakagawa & Santos, 2012). At present, no specific tests can assess heterogeneity in proportional meta-analyses (Barker et al., 2021). Thus, in this study, we used the most common heterogeneity statistic I^2 to calculate how much variation is attributable to each of the four random factors within the meta-analysis (Nakagawa & Santos, 2012). I^2 values of 25%, 50% and 75% are regarded as low, moderate and high, respectively (Higgins et al., 2003).

The effect of the four moderators was tested by adding them to the multilevel random-effects model described previously. Each model included study, species, phylogeny and observation ID as random effects, as well as the moderator variables as a categorical (regenerative capacity, relative weapon size and ramming behaviour) or continuous fixed effect (allometric slope). In addition, the Q_M statistic was used to determine whether the mean effect size differed significantly between the moderator categories (Koricheva et al., 2013). For analyses with categorical moderator variables, mixed-effect models were also run with the intercept removed and the double arcsine proportions were back transformed to estimate the mean effect size for each category (e.g. regenerative or non-regenerative). For the analyses on ramming behaviour and weapon allometry, pruned trees that only included species in the restricted data sets were used (25 and 40 effect sizes, respectively).

Signs of publication bias were not tested because these analyses are not recommended for proportional meta-analyses (Barker et al., 2021; Wang, 2023). The studies included in proportional meta-analyses report the proportion or prevalence of an event (e.g. injury); therefore, the outcome of such studies cannot be classified as either significant or nonsignificant. Papers that report low proportions should be as likely to be published as those reporting high proportions, so the assumption of publication bias against weak or nonsignificant results is not necessarily true for proportional studies.

Ethical Note

Due to the nature of this study, no ethical approval was required.

RESULTS

Our final data set included 82 effect sizes from 74 species, 13 orders and 36 studies (Fig. 1). Most of the effect sizes came from insects (49%) and mammals (41%), but we also obtained a few effect sizes for crustaceans, birds and an amphibian. Of the 82 observations included in our analyses, hummingbird bills, turkey spurs, cervid antlers, rhinoceros horns and crab claws can be regenerated (15.9% of effect sizes), while the remaining weapons are non-regenerative (84.1% of effect sizes). The data set was characterized by high total heterogeneity (total $I^2 = 97.1\%$), with 60.4% of the variance attributable to differences in studies, 27.1% to differences in phylogenetic history, <0.1% to differences in species and 9.7% to observation-level differences.

The overall proportion of weapon damage across all observations was 9.4% (random-effects model: 95% CI = [2.5%–20.0%]; Fig. 1). However, the prevalence of weapon damage was significantly influenced by regenerative capacity ($Q_M = 7.1$; $P = 0.008$; marginal $R^2 = 0.11$; Fig. 2). Damage was more common in species that can regenerate their weapons (20.3%; 95% CI = [8.7%–35.1%]) compared with species that lack regenerative capabilties (6.3%; 95% CI = [1.2%–14.5%]).

We found a significant effect of ramming behaviour on the prevalence of weapon damage ($Q_M = 3.9$; $P = 0.05$; marginal $R^2 = 0.04$), but it was in the opposite direction than what we predicted if rapid and forceful blows increase the risk of weapon failure (Fig. 3). On the contrary, species that use their weapons to ram opponents had slightly lower rates of damage (14.1%; 95% CI = [2.1%–33.4%]) than those that do not fight by ramming (22.1%; 95% CI = [6.2%–43.7%]).

Finally, we found no evidence that the prevalence of weapon damage was influenced by relative weapon size (Fig. S3; $Q_M = 0.18$; $P = 0.67$; marginal $R^2 = 0.001$) or the allometric slope of the weapon (Fig. S4; $Q_M = 2.43$; $P = 0.12$; marginal $R^2 = 0.03$).

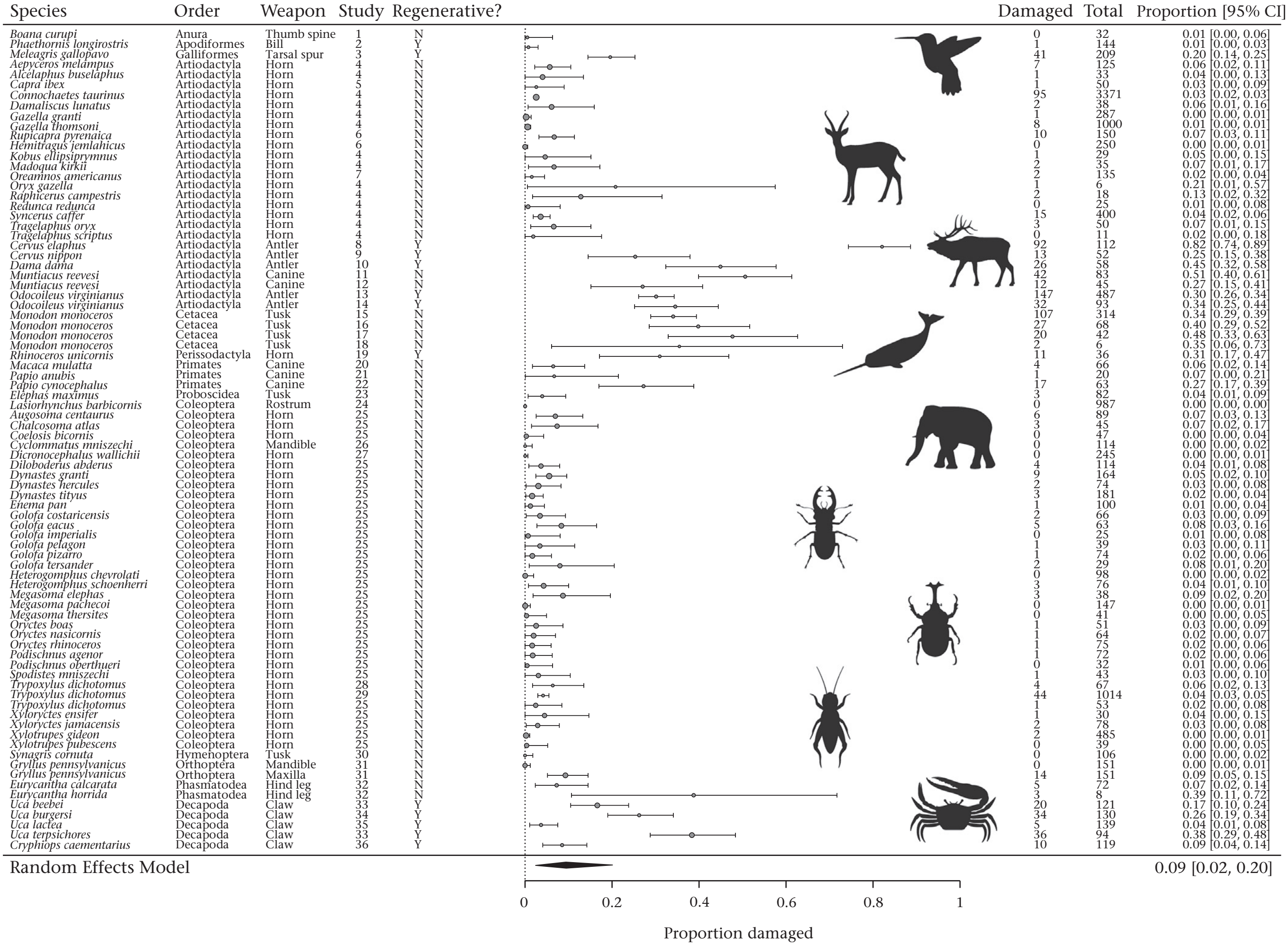
DISCUSSION

Our meta-analysis, which includes 82 effect sizes across 74 species and 13 orders, is the first systematic survey of the prevalence of weapon damage across the animal kingdom. We found that weapon damage was remarkably common, with an average of nearly 10% of males in a population suffering some degree of weapon damage. The severity of the reported damage ranged from punctured claws (fiddler crabs) to broken antler tines (deer) to the loss of entire horns (rhinoceros beetles). We suspect the observations in our data set may underestimate the true prevalence of weapon damage, as damaged individuals are typically overlooked or unreported. For example, several estimates of weapon damage were collected for the rhinoceros beetle, *T. dichotomus* (Fig. 1), and we found that the estimate based on museum specimens (2%; McCullough et al., 2015) was lower than that based on field observations (4% and 6%; McCullough, 2014; Siva-Jothy, 1987). These patterns are consistent with the hypothesis that damaged individuals are overlooked by field collectors and therefore, underrepresented in museum collections. Overall, our results indicate that weapon damage is a widespread phenomenon that is likely to influence the evolution of weapons and fighting behaviour within and among species.

Factors Influencing the Likelihood and Costs of Weapon Damage

Regenerative capacity

For species in which weapons are a key component of resource holding potential, substantial weapon damage will directly impact fitness (Arnott & Elwood, 2009; Lincoln, 1972). Damage to or complete loss of a weapon will result in an immediate reduction in resource holding potential, rendering damaged individuals less able to secure and defend access to mates and resources. Unless individuals can regain access to mates via alternative tactics (e.g. sneaking), the fitness of damaged individuals will essentially be ‘frozen’ at the time of damage, and all subsequent mating opportunities will be lost. Weapon damage will be especially detrimental if it occurs early in the mating season or early in life, when the number of attained matings is low and number of future mating opportunities potentially lost is high. However, if individuals can regenerate a broken weapon, they can limit the number of missed mating opportunities by restoring their resource holding potential (Fig. 4). We found that regenerative capacity was a significant predictor of the prevalence of weapon damage, with higher rates of damage in species that can regenerate their weapons compared to species that lack regenerative capabilities. This pattern is consistent



Species	Order	Weapon	Study	Regenerative?	Damaged	Total	Proportion [95% CI]
Boana curupi	Anura	Thumb spine	1	N	0	32	0.01 [0.00, 0.06]
Phaethornis longirostris	Apodiformes	Bill	2	Y	1	144	0.01 [0.00, 0.03]
Meleagris gallopavo	Galliformes	Tarsal spur	3	Y	41	209	0.20 [0.14, 0.25]
Aepyceros melampus	Artiodactyla	Horn	4	N	7	125	0.06 [0.02, 0.11]
Alcelaphus buselaphus	Artiodactyla	Horn	4	N	1	33	0.04 [0.00, 0.13]
Capra ibex	Artiodactyla	Horn	5	N	1	50	0.03 [0.00, 0.09]
Connochaetes taurinus	Artiodactyla	Horn	4	N	95	3371	0.03 [0.02, 0.03]
Damaliscus lunatus	Artiodactyla	Horn	4	N	2	38	0.06 [0.01, 0.16]
Gazella granti	Artiodactyla	Horn	4	N	1	287	0.00 [0.00, 0.01]
Gazella thomsoni	Artiodactyla	Horn	4	N	8	1000	0.01 [0.00, 0.01]
Rupicapra pyrenaica	Artiodactyla	Horn	6	N	10	150	0.07 [0.03, 0.11]
Hemitragus jemlahicus	Artiodactyla	Horn	6	N	0	250	0.00 [0.00, 0.01]
Kobus ellipsiprymnus	Artiodactyla	Horn	4	N	1	29	0.05 [0.00, 0.15]
Madoqua kirkii	Artiodactyla	Horn	4	N	2	35	0.07 [0.01, 0.17]
Oreamnos americanus	Artiodactyla	Horn	7	N	2	135	0.02 [0.00, 0.04]
Oryx gazella	Artiodactyla	Horn	4	N	1	6	0.21 [0.01, 0.57]
Raphicerus campestris	Artiodactyla	Horn	4	N	2	18	0.13 [0.02, 0.32]
Redunca redunca	Artiodactyla	Horn	4	N	0	25	0.01 [0.00, 0.08]
Syncerus caffer	Artiodactyla	Horn	4	N	15	400	0.04 [0.02, 0.06]
Tragelaphus oryx	Artiodactyla	Horn	4	N	3	50	0.07 [0.01, 0.15]
Tragelaphus scriptus	Artiodactyla	Horn	4	N	0	11	0.02 [0.00, 0.18]
Cervus elaphus	Artiodactyla	Antler	8	Y	92	112	0.82 [0.74, 0.89]
Cervus nippon	Artiodactyla	Antler	9	Y	13	52	0.25 [0.15, 0.38]
Dama dama	Artiodactyla	Antler	10	Y	26	58	0.45 [0.32, 0.58]
Muntiacus reevesi	Artiodactyla	Canine	11	N	42	83	0.51 [0.40, 0.61]
Muntiacus reevesi	Artiodactyla	Canine	12	N	12	45	0.27 [0.15, 0.41]
Odocoileus virginianus	Artiodactyla	Antler	13	Y	147	487	0.30 [0.26, 0.34]
Odocoileus virginianus	Artiodactyla	Antler	14	Y	32	93	0.34 [0.25, 0.44]
Monodon monoceros	Cetacea	Tusk	15	N	107	314	0.34 [0.29, 0.39]
Monodon monoceros	Cetacea	Tusk	16	N	27	68	0.40 [0.29, 0.52]
Monodon monoceros	Cetacea	Tusk	17	N	20	42	0.48 [0.33, 0.63]
Monodon monoceros	Cetacea	Tusk	18	N	2	6	0.35 [0.06, 0.73]
Rhinoceros unicornis	Perissodactyla	Horn	19	Y	11	36	0.31 [0.17, 0.47]
Macaca mulatta	Primates	Canine	20	N	4	66	0.06 [0.02, 0.14]
Papio anubis	Primates	Canine	21	N	1	20	0.07 [0.00, 0.21]
Papio cynocephalus	Primates	Canine	22	N	17	63	0.27 [0.17, 0.39]
Elephas maximus	Proboscidea	Tusk	23	N	3	82	0.04 [0.01, 0.09]
Lasiorhynchus barbicornis	Coleoptera	Rostrum	24	N	0	987	0.00 [0.00, 0.00]
Augosoma centaurus	Coleoptera	Horn	25	N	6	89	0.07 [0.03, 0.13]
Chalcosoma atlas	Coleoptera	Horn	25	N	3	45	0.07 [0.02, 0.17]
Coelosis bicornis	Coleoptera	Horn	25	N	0	47	0.00 [0.00, 0.04]
Cyclommatus mniszechi	Coleoptera	Mandible	26	N	0	114	0.00 [0.00, 0.02]
Dicronocephalus wallichii	Coleoptera	Horn	27	N	0	245	0.00 [0.00, 0.01]
Diloboderus abderus	Coleoptera	Horn	25	N	4	114	0.04 [0.01, 0.08]
Dynastes granti	Coleoptera	Horn	25	N	9	164	0.05 [0.02, 0.10]
Dynastes hercules	Coleoptera	Horn	25	N	2	74	0.03 [0.00, 0.08]
Dynastes tityus	Coleoptera	Horn	25	N	3	181	0.02 [0.00, 0.04]
Enema pan	Coleoptera	Horn	25	N	1	100	0.01 [0.00, 0.04]
Golofa costaricensis	Coleoptera	Horn	25	N	2	66	0.03 [0.00, 0.09]
Golofa eacus	Coleoptera	Horn	25	N	5	63	0.08 [0.03, 0.16]
Golofa imperialis	Coleoptera	Horn	25	N	0	25	0.01 [0.00, 0.08]
Golofa pelagon	Coleoptera	Horn	25	N	1	39	0.03 [0.00, 0.11]
Golofa pizarro	Coleoptera	Horn	25	N	1	74	0.02 [0.00, 0.06]
Golofa tersander	Coleoptera	Horn	25	N	2	29	0.08 [0.01, 0.20]
Heterogomphus chevrolati	Coleoptera	Horn	25	N	0	98	0.00 [0.00, 0.02]
Heterogomphus schoenherri	Coleoptera	Horn	25	N	3	76	0.04 [0.01, 0.10]
Megasoma elephas	Coleoptera	Horn	25	N	3	38	0.09 [0.02, 0.20]
Megasoma pachecoi	Coleoptera	Horn	25	N	0	147	0.00 [0.00, 0.01]
Megasoma thersites	Coleoptera	Horn	25	N	0	41	0.00 [0.00, 0.05]
Oryctes boas	Coleoptera	Horn	25	N	1	51	0.03 [0.00, 0.09]
Oryctes nasicornis	Coleoptera	Horn	25	N	1	64	0.02 [0.00, 0.07]
Oryctes rhinoceros	Coleoptera	Horn	25	N	1	75	0.02 [0.00, 0.06]
Podischnus agenor	Coleoptera	Horn	25	N	1	72	0.02 [0.00, 0.06]
Podischnus oberthueri	Coleoptera	Horn	25	N	0	32	0.01 [0.00, 0.06]
Spodistes mniszechi	Coleoptera	Horn	25	N	1	43	0.03 [0.00, 0.10]
Trypoxylus dichotomus	Coleoptera	Horn	28	N	4	67	0.06 [0.02, 0.13]
Trypoxylus dichotomus	Coleoptera	Horn	29	N	44	1014	0.04 [0.03, 0.05]
Trypoxylus dichotomus	Coleoptera	Horn	25	N	1	53	0.02 [0.00, 0.08]
Xyloryctes ensifer	Coleoptera	Horn	25	N	1	30	0.04 [0.00, 0.15]
Xyloryctes jamacensis	Coleoptera	Horn	25	N	2	78	0.03 [0.00, 0.08]
Xylotrupes gideon	Coleoptera	Horn	25	N	2	485	0.00 [0.00, 0.01]
Xylotrupes pubescens	Coleoptera	Horn	25	N	0	39	0.00 [0.00, 0.05]
Synagris cornuta	Hymenoptera	Tusk	30	N	0	106	0.00 [0.00, 0.02]
Gryllus pennsylvanicus	Orthoptera	Mandible	31	N	0	151	0.00 [0.00, 0.01]
Gryllus pennsylvanicus	Orthoptera	Maxilla	31	N	14	151	0.09 [0.05, 0.15]
Eurycantha calcarata	Phasmatodea	Hind leg	32	N	5	72	0.07 [0.02, 0.14]
Eurycantha horrida	Phasmatodea	Hind leg	32	N	3	8	0.39 [0.11, 0.72]
Uca beebei	Decapoda	Claw	33	Y	20	121	0.17 [0.10, 0.24]
Uca burgersi	Decapoda	Claw	34	Y	34	130	0.26 [0.19, 0.34]
Uca lactea	Decapoda	Claw	35	Y	5	139	0.04 [0.01, 0.08]
Uca terpsichores	Decapoda	Claw	33	Y	36	94	0.38 [0.29, 0.48]
Cryphiops caementarius	Decapoda	Claw	36	Y	10	119	0.09 [0.04, 0.14]
Random Effects Model							0.09 [0.02, 0.20]

Figure 1. Forest plot comparing the prevalence of weapon damage amongst species that can and cannot regenerate their weapons. Proportions and 95% CIs are estimated from back transformation of the random-effect meta-regression model. Larger circles and smaller CIs denote studies with larger sample sizes. Silhouettes illustrate the organismal diversity included in our data set (from top to bottom): hummingbird, gazelle, elk, narwhal, elephant, stag beetle, rhinoceros beetle, cricket and fiddler crab. Study ID indicates data from the same study: 1: Candaten et al. (2020); 2: Rico-Guevara and Araya-Salas (2015); 3: Badyaev et al. (1998); 4; Packer (1983); 5: Bergeron et al. (2010); 6: Lovari et al. (2009); 7: Côté et al. (1998); 8: Johnson et al. (2005); 9: Hayden et al. (1994); 10: Jennings et al. (2017); 11: Chapman (1997); 12: Pei (1996); 13: Karns and Ditchkoff (2012); 14: Jin and Shipman (2010); 15: Porsild (1922); 16: Silverman and Dunbar (1980); 17: Gerson and Hickie (1985); 18: Nweeia et al. (2014); 19: Dinerstein (1991); 20: Kimock et al. (2022); 21: Packer (1979); 22: Galbany et al. (2015); 23: Chelliah and Sukumar (2013); 24: Painting and Holwell (2013); 25: McCullough et al. (2015); 26: Chen et al. (2022); 27: Kojima and Lin (2017); 28: Siva-Jothy (1987); 29: McCullough (2014); 30: Longair (2004); 31: Judge and Bonanno (2008); 32: Boisseau et al. (2020); 33: Dennenmoser and Christy (2013); 34: A. R. Jones (1980); 35: Muramatsu and Koga (2016); 36: Rojas et al. (2012).

with the hypothesis that the costs of weapon damage are lower for regenerative species.

There is considerable variation in regenerative capability across the animal kingdom (Zhao et al., 2016), and this variation extends to the regrowth of damaged weapons. Species not only differ in whether or not they can regenerate their weapons but also, among regenerative species, in the timing of regeneration, the amount of the weapon that can be regenerated and the quality of the new weapon (Fig. 5).

Some species can regrow a damaged weapon, but the regenerated weapon is inferior to the original weapon in form and/or function. For example, male fiddler crabs can autotomize and regrow damaged limbs, including their major claw that is used both as a weapon during male–male fights and as a signal to attract females and deter rivals (Dennenmoser & Christy, 2013). However, the regenerated claw is permanently lighter, weaker and more fragile than the original claw (Backwell et al., 2000; Lailvaux et al., 2009). Males with regenerated claws can use bluffing tactics to deter opponents (Backwell et al., 2000), but they surrender quickly if a fight escalates because the regenerated claws are weaker (Muramatsu & Koga, 2016; Tina & Keeratipattarakarn, 2019), and they usually lose contests against males with original claws (McLain et al., 2010). The regeneration of a weaker weapon has similar consequences in the virile crayfish, *Faxonius virilis*, in which the regenerated weapon is equal in size to the original but has reduced muscle mass and therefore produces significantly weaker pinching forces (Graham et al., 2021). These examples suggest that although regeneration of a weaker weapon allows males to regain some mating success, males will never fully restore their initial resource holding potential (Fig. 4c). The exact fitness ramifications of this change will depend on the difference between the original and regenerated weapon and a male's ability to compensate for this competitive disadvantage by altering his fighting strategies.

Other species can regenerate a weapon that is equivalent to the original in form and function, which means that resource holding potential is fully restored once regeneration is completed. Such

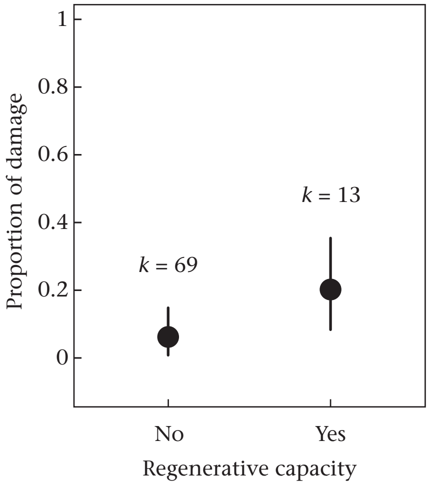


Figure 2. Difference in the prevalence of weapon damage for species that can and cannot regenerate their weapons. Black points represent the estimated prevalences, and black bars represent 95% CIs. *k* indicates the number of effect sizes in each category.

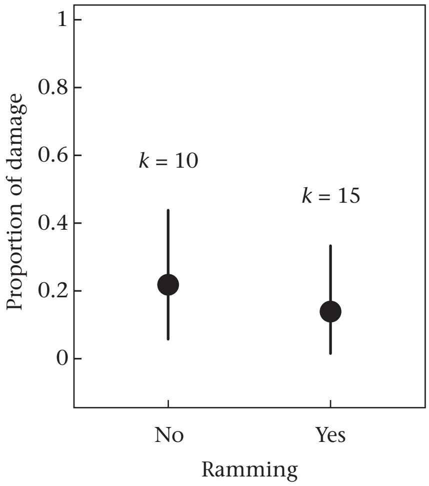


Figure 3. Difference in the prevalence of weapon damage for species that do and do not fight by ramming. Black points represent the estimated prevalences, and black bars represent 95% CIs. *k* indicates the number of effect sizes in each category.

species fall into three main categories. (1) Those that regenerate weapons in response to damage. (2) Those that shed and regrow weapons cyclically, regardless of whether damage has been sustained. (3) Those that continuously grow their weapons throughout their lifetime. These categories differ in the timing of regeneration, which is a key consideration given that the time required to regain fighting ability determines the magnitude of lost mating opportunities (Fig. 4).

In many crustaceans, weapon regeneration begins as soon as the original weapon is damaged and autotomized. This rapid onset of regeneration is expected to minimize the fitness cost of weapon damage, but even in these systems, full regeneration can require a substantial investment of energy and time. For example, snapping shrimp only need one moult cycle to regain their ability to produce snaps after a claw is autotomized, but they require seven additional moults to regenerate the shape and musculature of a fully functional claw (Mellon, 1999; Pereira et al., 2014).

Cervids are the only family of animals that shed and regrow their weapons annually (Lincoln, 1992). This yearly cycle of renewal has clear advantages: antler size can increase with age as new sets are grown (Lincoln, 1992), and males can adjust their investment in antler production in response to changing levels of reproductive competition (Carranza et al., 2020). However, considering that the timing of regeneration is fixed, the consequences of weapon damage will vary depending on when the damage occurs within the mating season (Fig. 4b). If a stag damages his antlers late in the rut, then he may suffer almost no loss in mating success, whereas a stag that damages his antlers early in the rut may lose out on a whole season of mating opportunities. This variation is likely to affect fighting decisions and the propensity to escalate across the breeding season.

Finally, some weapons, such as the horns of rhinoceroses and bills and tarsal spurs of birds, are made of keratin that grow continuously, similar to human fingernails (Badyaev et al., 1998; Hieronymus et al., 2006; Rico-Guevara & Araya-Salas, 2015). This continuous growth is expected to minimize the fitness costs of weapon damage because a worn or broken weapon will eventually grow back to its fully functional form (Fig. 4a). In the hummingbird, *Phaethornis longirostris*, males use their bills as daggers to defend territories in a lek (Rico-Guevara & Araya-Salas, 2015). In one study, researchers observed that a male with a broken bill tip had lost his territory from the previous year, but regained his territory the following year after his bill tip had grown back to its original size (Rico-Guevara & Araya-Salas, 2015). This finding highlights the fitness benefit of being able to replace a broken weapon to maintain

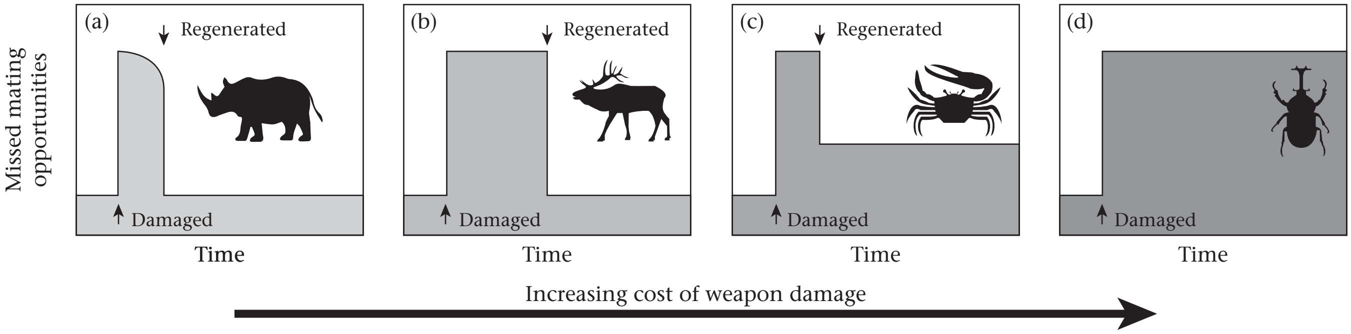


Figure 4. Variation in the cost of weapon damage. Weapon damage reduces an individual's ability to secure mating opportunities. Therefore, the cost of damage depends on if, when and to what degree an individual can regenerate its weapon and restore its resource holding potential. (a) Individuals that continuously grow their weapons (e.g. rhinoceroses) or can immediately regenerate a weapon that is equally strong as the original (e.g. snapping shrimp) will incur the smallest fitness cost. (b) Individuals that can regenerate an equally strong weapon, but only at the start of a new breeding season (e.g. red deer), will incur a greater fitness cost. (c) Individuals that regenerate a weapon that is weaker than the original (e.g. fiddler crabs) will incur a greater fitness cost. (d) Individuals that cannot regenerate their weapons (e.g. rhinoceros beetles) will incur the highest fitness cost.

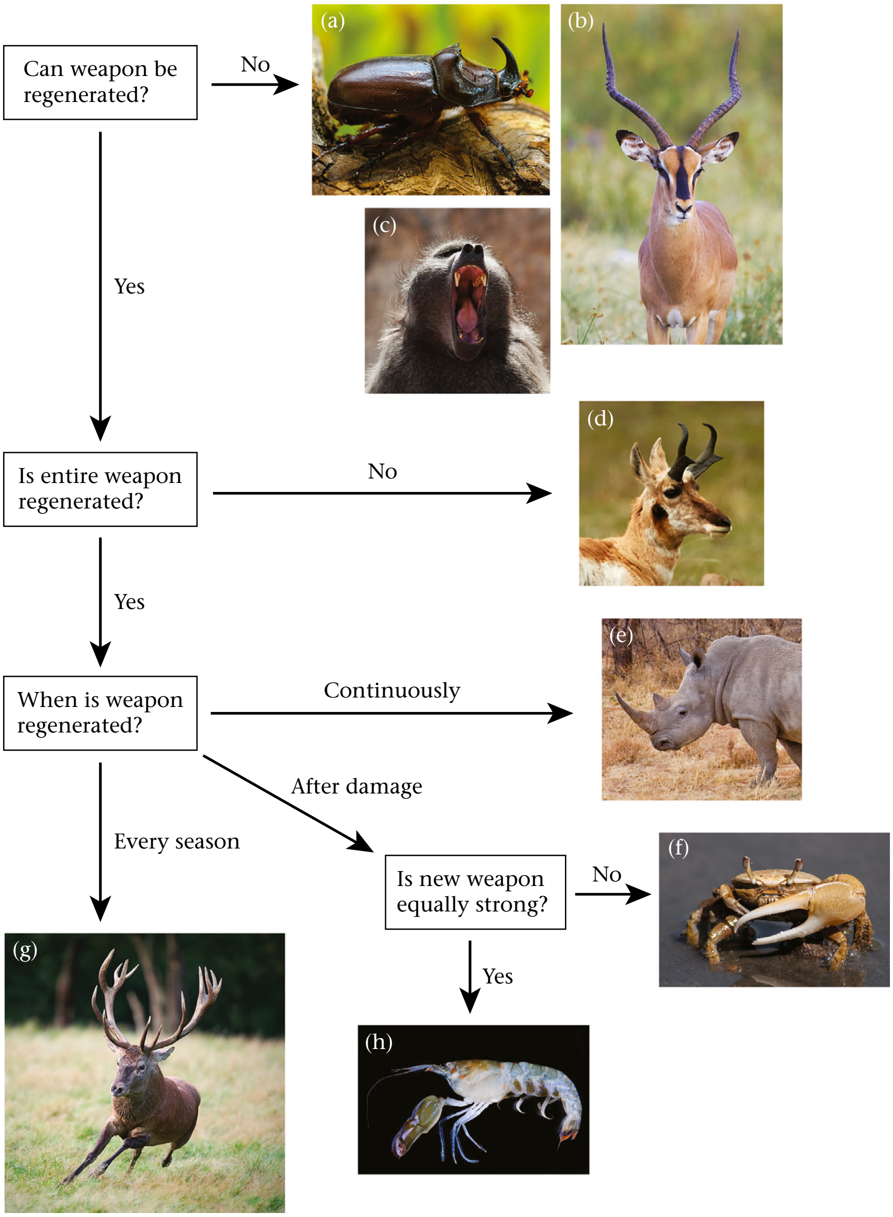


Figure 5. Variation in the capacity for weapon regeneration. (a) Beetle horns, (b) bovid horns and (c) primate canines cannot be regenerated. (d) The horn sheath of pronghorns is regenerated each season, but the bony core is not. (e) Rhinoceros horns, (f) fiddler crab claws, (g) ungulate antlers and (h) snapping shrimp claws can be regenerated, but the timing of regeneration differs among taxa. Rhinoceros horns grow continuously. Fiddler crabs and shrimp regenerate their weapon after it is autotomized, for example after severe damage. Ungulate antlers are shed and regenerated every season, regardless of the state of weapon damage. Regenerated claws in fiddler crabs are weaker and more slender than original claws, whereas regenerated claws in snapping shrimp are identical to their original counterparts. All photos from Wikimedia Commons. All photos are available from Wikimedia Commons. Photo credit and licence (a–h): Andrew Biks (CC BY 4.0), Yathin S Krishnappa (CC BY-SA 3.0), David Rosen (CC BY 2.0), Frank Schulenburg (CC BY-SA 3.0), Ikiwaner (GFDL 1.2), Wilfredo Rodríguez (CCO 1.0), Luc Viatour (CC BY-SA 3.0), TY Chan and CW Lin (CC BY 4.0).

or regain resource holding potential and minimize lost mating opportunities. We did not have enough samples to include these categories in our meta-analyses, but we encourage future studies to compare rates of weapon damage among species with varying degrees of regenerative capabilities.

Weapon size

The relative size of sexually selected weapons varies dramatically within and among species (O'Brien et al., 2018), and this variation is expected to influence the likelihood of weapon damage. In most species, sexually selected weapons can be modelled as a cylindrical beam that is fixed at one end (e.g. the head) and free at the other, where fighting forces are applied (Kitchener, 1991). Larger weapons result in longer moment arms, so, these structures will experience higher bending stresses during fights and face a higher risk of failure (Kitchener, 1991). Most sexually selected weapons scale disproportionately with body size (Emlen, 2008; McCullough & O'Brien, 2022). Therefore, larger individuals typically have relatively larger weapons compared with smaller individuals and thus, a higher likelihood of serious weapon damage.

Contrary to our predictions, we found no evidence that the prevalence of weapon damage was influenced by relative weapon size. Weapon damage was equally common among species with relatively large weapons as among species with relatively small weapons. In contrast to these meta-regression results, our literature search identified several studies that reported larger individuals suffering from higher rates of weapon damage than smaller individuals (Table S2). As most studies do not explicitly compare the size distribution between damaged and undamaged individuals, it is possible that this pattern is even more widespread. Collectively, these results suggest that weapon exaggeration increases the risk of weapon failure within some species but not among species.

Fighting style

Considering that the cuticle, bone and keratin that make up sexually selected weapons are (like all biomaterials) viscoelastic, the ways in which species use their weapons during fights can affect the likelihood of weapon failure. Viscoelastic materials become more rigid and brittle in response to fast loading rates, so a rapid flick or clash may put weapons at a high risk of catastrophic failure (Currey, 1967; Wainwright et al., 1976). Compared with tough materials, brittle materials absorb less energy. Therefore, cracks can spread easily, especially in the presence of microcracks, scratches and other surface flaws.

Contrary to our prediction that rapid and forceful blows (i.e. ramming) would increase the risk of weapon damage, we found that ramming behaviour was associated with a decreased risk of weapon damage. Among artiodactyls (the only group in our meta-analysis with detailed published descriptions of fighting behaviour), species that use their weapons to ram opponents had slightly lower rates of damage than those that do not ram. We hypothesize that ramming behaviour selects for tougher materials, which will make weapons less prone to damage during fights. This unexpected result highlights how fighting behaviour and the risk of weapon damage can interact in complex ways to influence the evolution of weapon morphology.

Weapon allometry

The structures used in male—male competition can be considered as part of a continuum, with pure weapons that are used exclusively in physical fights at one extreme, and pure signals that are used exclusively to threaten and assess rivals at the other (McCullough et al., 2016). Compared with pure weapons, pure signals are more exaggerated, and have steeper allometric slopes (McCullough & O'Brien, 2022). Species with pure weapons are also expected to rapidly escalate to all-out fighting without any prior signalling (Candaten et al., 2020), whereas species with pure signals are expected to engage in lengthy, stereotyped displays to assess the resource holding potential of opponents before engaging in a potentially risky fight (Barrette & Vandal, 1990). The risk of weapon damage is therefore, expected to vary along the weapon—signal continuum because of differences in fighting behaviour and the relative importance of fighting versus signalling.

Given their smaller and more proportional size, we predicted that pure weapons (shallow allometries) would be less susceptible to damage than pure signals (steep allometries). On the contrary, no relationship was found between weapon allometry and the prevalence of weapon damage. However, future work is necessary to confirm whether allometric slope is a good predictor of a structure's position along the weapon—signal continuum, or the relative importance of fighting versus signalling (McCullough & O'Brien, 2022).

Mechanical properties

Although we did not have sufficient data to include mechanical properties in our meta-analysis, we discuss it here as an additional factor that may influence the likelihood and costs of weapon damage. Weapons have been selected to be strong and stiff structures during combat, and the mechanical properties of present-day weapons are well-suited for their fighting functions (Currey, 1979; Currey et al., 2009; McCullough et al., 2014). However, weapon development is highly sensitive to nutrition (Emlen & Nijhout, 2000; Johns et al., 2014, Jones et al., 2018). Therefore, variation in diet and other environmental conditions can affect the structural integrity of weapons and make them more (or less) susceptible to damage. For example, antler bone has the highest work of fracture among mammalian bone tissue (Currey, 1979), which means that it is remarkably tough and can absorb high-impact forces without breaking. These material properties are largely attributable to the low mineral content of antlers (Currey, 1979), and variation in mineralization levels among seasons, populations or species can influence the likelihood of weapon damage (Picavet & Balligand, 2016). For example, in a Spanish population of red deer, *C. elaphus*, antlers grown after an unusually cold winter were significantly more brittle and fractured more frequently than those grown after a ‘normal’ winter (Landete-Castillejos et al., 2010). The fact that high rates of antler damage were not observed among captive deer from a nearby farm that were fed whole meal suggests that the reduction in antler toughness was primarily driven by changes in diet rather than climate (Landete-Castillejos et al., 2010). Similarly, in leaf-footed bugs, *Narnia femorata*, males raised on a higher quality diet (mature green cactus fruit) developed hind femur weapons that were more puncture resistant than those raised on a low-quality diet (immature green cactus fruit; Woodman et al., 2021). Thus, fluctuations in the chemical composition and/or nutritional value of plants that comprise an animal's diet can have cascading effects on the structural integrity of the animal's weapons (Johnson et al., 2007; Landete-Castillejos et al., 2010; Woodman et al., 2021).

Variation in the overall structure of weapons can also influence their likelihood of damage. For example, across African bovids, there is a negative correlation between horn thickness and horn breakage, with the highest rates of broken horns found in species with relatively thin horns (Packer, 1983). Fewer studies have compared the mechanical properties of sexually selected weapons in arthropods. However, the fact that cuticle thickness varies among species (e.g. rhinoceros beetle horns (McCullough et al., 2015) and crab claws (Palmer et al., 1999; Swanson et al., 2013)) indicates that the architecture of these structures has been selected to optimize strength and stiffness. Weapon structure also varies intraspecifically. Within three species of crustaceans, larger claws are known to be composed of proportionately less soft (muscle) tissue and proportionately more exoskeleton than smaller claws, which may represent an adaptation to minimize energetic maintenance costs (Dinh, 2022). Although the study did not specifically measure cuticle thickness, increasing exoskeleton mass should make claws stronger and tougher, suggesting that high proportions of metabolically inexpensive exoskeleton may also represent an adaptation to minimize weapon damage.

Lastly, and perhaps most importantly, animal weapons may be more likely to break if they develop scratches, abrasions, microcracks or other types of wear (McCullough, 2014). These surface defects can serve as local stress concentrators and significantly reduce the maximum load that can be sustained before failure (Boulding & LaBarbera, 1986; Dirks et al., 2013; Wainwright et al., 1976). In our literature search, several studies have noted that broken weapons were more common at the end of the breeding season, including Asian rhinoceros beetles (McCullough, 2014), tule elk (Johnson et al., 2005) and sika deer (Hayden et al., 1994). These results are consistent with the hypothesis that these weapons ultimately failed by fatigue fracture after males had engaged in a full season of intense fighting and subjected their weapons to high, repeated loads. An alternative hypothesis is that repeated fighting means that males simply have accumulated more chances to break their weapon by the end of the mating season.

Consequences of Weapon Damage for Fighting Behaviour

Theoretical models of animal contests, such as the cumulative assessment model, predict that an individual's decision to persist, escalate or flee from a fight will depend on the costs accumulated during the fight (Arnott & Elwood, 2009; Payne, 1998). In particular, the cumulative assessment model posits that an individual will persevere in a fight until the energy expended and/or physical damage incurred from the contest (including self-inflicted injuries) exceeds the individual's maximum cost threshold (Lane & Briffa, 2017; Payne, 1998). Although participation in any contest requires an energetic investment, only those that escalate to an all-out fight pose a risk of weapon damage. Individuals can therefore limit their risk of injury by settling fights before they escalate to physical violence. As a result, we expect that the likelihood and cost of weapon damage will affect the probability of contest escalation, leading to variation in fighting behaviours at both individual and species level. Specifically, we predict that when the risk of weapon damage is high (i.e. high likelihood and/or cost), individuals will be cautious about engaging in physical fights, and most contests will be settled noninjuriously (e.g. via signalling). Conversely, when the risk of weapon damage is low (i.e. low likelihood and/or cost), individuals will rapidly escalate to physical fighting as soon as they are confronted with an opponent.

Among species, we expect variation in the frequency and speed of contest escalation to covary with regenerative capacity. Specifically, we expect species that can regenerate equally strong weapons (for whom the cost of weapon damage is lowest) to escalate to injurious fighting more rapidly and more frequently than species that cannot regenerate their weapons (for whom the cost of weapon damage is greatest). The likelihood of weapon damage should also influence fighting decisions, regardless of the capacity for weapon regeneration. We encourage future research to explore how variation in the structural integrity of weapons affects fighting behaviour and fighting outcomes (McEvoy et al., 2024; Woodman et al., 2021).

Within species, we expect the frequency and speed of contest escalation to vary across a season depending on an individual's expected cost of weapon damage. For example, male rhinoceros beetles that cannot regenerate their horns may become more cautious about engaging in a fight if their horns have been extensively scratched or worn from previous battles. Males may therefore, gauge the likelihood of catastrophic weapon damage over the course of their lifetime and adjust their fighting decisions accordingly, for example by lowering their maximum cost threshold (Lane & Briffa, 2017). However, the degree to which an individual will factor the likelihood and cost of weapon damage into its contest decisions may depend on the information about resource holding potential available to each contestant (e.g. self-assessment or mutual assessment; Arnott & Elwood, 2009). Collectively, these observations indicate that variation in the expected cost of weapon damage can influence the duration and escalation of contests within and among species and should be considered in animal contest theory.

CONCLUSION

In this paper, we highlight the important but underappreciated cost of sexually selected weapon damage. Although individuals can suffer devastating fitness consequences if they break their weapons and can no longer fight effectively to secure mating opportunities, the costs and consequences of weapon damage have largely been ignored. We demonstrate that weapon damage is remarkably common, with an average of 10% of males in a population suffering some degree of damage. We discuss how the fitness consequences of weapon damage depend on if, when, and to what degree a species can regenerate its weapon, as well as the extent to which these fitness consequences influence the evolution of weapon morphology and fighting behaviour within and among species. Unfortunately, our ability to resolve the evolutionary implications of weapon damage is currently impeded by a lack of data. Hence, we urge researchers to report observations of weapon damage and escalation rates in natural and lab-based populations, even if that value is zero. These data will facilitate comparative studies across species on the relationship between weapon damage and fighting behaviour, fostering new insights into male−male competition and the evolution of animal weapons.

Data availability

All data and code are available on GitHub (https://github.com/erinlouisa/weapon_damage).

CREDIT AUTHORSHIP CONTRIBUTION STATEMENT

Sarah M. Lane: Writing − review & editing, Writing − original draft, Formal analysis, Data curation, Conceptualization. **Erin L. McCullough:** Writing − review & editing, Writing − original draft, Formal analysis, Data curation.

Declaration of competing interest

The authors declare there are no conflicts of interest.

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Supplementary Material

Supplementary material associated with this article is available, at https://doi.org/10.1016/j.anbehav.2025.123117.

References

Allen, B. J., & Levinton, J. S. (2007). Costs of bearing a sexually selected ornamental weapon in a fiddler crab. *Functional Ecology, 21*(1), 154−161. https://doi.org/10.1111/j.1365-2435.2006.01219.x

Arnott, G., & Elwood, R. W. (2009). Assessment of fighting ability in animal contests. *Animal Behaviour, 77*(5), 991−1004. https://doi.org/10.1016/j.anbehav.2009.02.010

Backwell, P. R. Y., Christy, J. H., Telford, S. R., Jennions, M. D., & Passmore, J. (2000). Dishonest signalling in a fiddler crab. *Proceedings of the Royal Society of London B Biological Sciences, 267*(1444), 719−724. https://doi.org/10.1098/rspb.2000.1062

Badyaev, A. V., Etges, W. J., Faust, J. D., & Martin, T. E. (1998). Fitness correlates of spur length and spur asymmetry in male wild turkeys. *Journal of Animal Ecology, 67*(6), 845−852. https://doi.org/10.1046/j.1365-2656.1998.6760845.x

Barker, T. H., Migliavaca, C. B., Stein, C., Colpani, V., Falavigna, M., Aromataris, E., & Munn, Z. (2021). Conducting proportional meta-analysis in different types of systematic reviews: A guide for synthesisers of evidence. *BMC Medical Research Methodology, 21*(1), 189. https://doi.org/10.1186/s12874-021-01381-z

Barrette, C., & Vandal, D. (1990). Sparring, relative antler size, and assessment in male caribou. *Behavioral Ecology and Sociobiology, 26*(6), 383−387. https://doi.org/10.1007/bf00170894

Bergeron, P., Grignolio, S., Apollonio, M., Shipley, B., & Festa-Bianchet, M. (2010). Secondary sexual characters signal fighting ability and determine social rank in

Alpine ibex (*Capra ibex*). *Behavioral Ecology and Sociobiology, 64*(8), 1299–1307. https://doi.org/10.1007/s00265-010-0944-x

Boisseau, R. P., Ero, M. M., Makai, S., Bonneau, L. J. G., & Emlen, D. J. (2020). Sexual dimorphism divergence between sister species is associated with a switch in habitat use and mating system in thorny devil stick insects. *Behavioural Processes, 181*, Article 104263. https://doi.org/10.1016/j.beproc.2020.104263

Boulding, E. G., & LaBarbera, M. (1986). Fatigue damage: Repeated loading enables crabs to open larger bivalves. *Biological Bulletin, 171*(3), 538–547. https://doi.org/10.2307/1541622

Côté, S. D., Festa-Bianchet, M., & Smith, K. G. (1998). Horn growth in mountain goats (*Oreamnos americanus*). *Journal of Mammalogy, 79*(2), 406–414. https://doi.org/10.2307/1382971

Candaten, A., Possenti, A. G., Mainardi, Á. A., da Rocha, M. C., & Palaoro, A. V. (2020). Fighting scars: Heavier gladiator frogs bear more injuries than lighter frogs. *Acta Ethologica, 23*(1), 39–44. https://doi.org/10.1007/s10211-019-00333-7

Caro, T., Graham, C., Stoner, C., & Flores, M. (2003). Correlates of horn and antler shape in bovids and cervids. *Behavioral Ecology and Sociobiology, 55*(1), 32–41. https://doi.org/10.1007/s00265-003-0672-6

Carranza, J., Pérez-Barbería, J., Mateos, C., Alarcos, S., Torres-Porras, J., Pérez-González, J., Sánchez-Prieto, C. B., Valencia, J., Castillo, L., & de la Peña, E. (2020). Social environment modulates investment in sex trait versus lifespan: Red deer produce bigger antlers when facing more rivalry. *Scientific Reports, 10*(1), 9234. https://doi.org/10.1038/s41598-020-65578-w

Chapman, N. G. (1997). Upper canine teeth of *Muntiacus* (Cervidae) with particular reference to *M. reevesi*. *Zeitschrift Für Säugetierkunde, 62*, 32–36.

Chelliah, K., & Sukumar, R. (2013). The role of tusks, musth and body size in male–male competition among Asian elephants, Elephas maximus. *Animal Behaviour, 86*(6), 1207–1214. https://doi.org/10.1016/j.anbehav.2013.09.022

Chen, Z.-Y., Lin, C.-P., & Hsu, Y. (2022). Stag beetle *Cyclommatus mniszechi* employs both mutual-and self-assessment strategies in male-male combat. *Behavioural Processes, 202*, Article 104750. https://doi.org/10.1016/j.beproc.2022.104750

Cummings, M., Evans, H. K., & Chaves-Campos, J. (2018). Male horn dimorphism and its function in the Neotropical dung beetle *Sulcophanaeus velutinus*. *Journal of Insect Behavior, 31*(5), 471–489. https://doi.org/10.1007/s10905-018-9693-x

Currey, J. D. (1967). The failure of exoskeletons and endoskeletons. *Journal of Morphology, 123*(1), 1–16. https://doi.org/10.1002/jmor.1051230102

Currey, J. D. (1979). Mechanical properties of bone tissues with greatly differing functions. *Journal of Biomechanics, 12*(4), 313–319. https://doi.org/10.1016/0021-9290(79)90073-3

Currey, J. D., Landete-Castillejos, T., Estevez, J., Ceacero, F., Olguin, A., Garcia, A., & Gallego, L. (2009). The mechanical properties of red deer antler bone when used in fighting. *Journal of Experimental Biology, 212*(24), 3985–3993. https://doi.org/10.1242/jeb.032292

Dennenmoser, S., & Christy, J. H. (2013). The design of a beautiful weapon: Compensation for opposing sexual selection on a trait with two functions. *Evolution, 67*(4), 1181–1188. https://doi.org/10.1111/evo.12018

Dinerstein, E. (1991). Sexual dimorphism in the greater one-horned rhinoceros (*Rhinoceros unicornis*). *Journal of Mammalogy, 72*(3), 450–457. https://doi.org/10.2307/1382127

Dinh, J. P. (2022). Large and exaggerated sexually selected weapons comprise high proportions of metabolically inexpensive exoskeleton. *Biology Letters, 18*(2), Article 20210550. https://doi.org/10.1098/rsbl.2021.0550

Dirks, J.-H., Parle, E., & Taylor, D. (2013). Fatigue of insect cuticle. *Journal of Experimental Biology, 216*(10), 1924–1927. https://doi.org/10.1242/jeb.083824

Emberts, Z., Hwang, W. S., & Wiens, J. J. (2021). Weapon performance drives weapon evolution. *Proceedings of the Royal Society B: Biological Sciences, 288*, Article 20202898. https://doi.org/10.1098/rspb.2020.2898, 1943.

Emlen, D. J. (2001). Costs and the diversification of exaggerated animal structures. *Science, 291*(5508), 1534–1536. https://doi.org/10.1126/science.1056607

Emlen, D. J. (2008). The evolution of animal weapons. *Annual Review of Ecology, Evolution, and Systematics, 39*(1), 387–413. https://doi.org/10.1146/annurev.ecolsys.39.110707.173502

Emlen, D. J., & Nijhout, H. F. (2000). The development and evolution of exaggerated morphologies in insects. *Annual Review of Entomology, 45*(1), 661–708. https://doi.org/10.1146/annurev.ento.45.1.661

Fuchikawa, T., & Okada, K. (2013). Inter- and intrasexual genetic correlations of exaggerated traits and locomotor activity. *Journal of Evolutionary Biology, 26*(9), 1979–1987. https://doi.org/10.1111/jeb.12197

Galbany, J., Tung, J., Altmann, J., & Alberts, S. C. (2015). Canine length in wild male baboons: Maturation, aging and social dominance rank. *PLoS One, 10*(5), Article e0126415. https://doi.org/10.1371/journal.pone.0126415

Gerson, H. B., & Hickie, J. P. (1985). Head scarring on male narwhals (*Monodon monoceros*): Evidence for aggressive tusk use. *Canadian Journal of Zoology, 63*(9), 2083–2087. https://doi.org/10.1139/z85-306

Goyens, J., Dirckx, J., & Aerts, P. (2015). Costly sexual dimorphism in *Cyclommatus metallifer* stag beetles. *Functional Ecology, 29*(1), 35–43. https://doi.org/10.1111/1365-2435.12294

Graham, Z. A., Vargas, C., Angilletta Jr, M. J., & Palaoro, A. V. (2021). Regenerated claws of the virile crayfish *Faxonius virilis* (Hagen, 1870) (Decapoda: Astacidea: Cambaridae) generate weaker pinching forces compared to original claws. *Journal of Crustacean Biology, 41*(3), Article ruab036.

Hayden, T. J., Lynch, J. M., & O'Corry-Crowe, G. (1994). Antler growth and morphology in a feral sika deer (*Cervus nippon*) population in Killarney, Ireland. *Journal of Zoology, 232*(1), 21–35. https://doi.org/10.1111/j.1469-7998.1994.tb01557.x

Hieronymus, T. L., Witmer, L. M., & Ridgely, R. C. (2006). Structure of white rhinoceros (*Ceratotherium simum*) horn investigated by X-ray computed tomography and histology with implications for growth and external form. *Journal of Morphology, 267*(10), 1172–1176. https://doi.org/10.1002/jmor.10465

Higgins, J. P. T., Thompson, S. G., Deeks, J. J., & Altman, D. G. (2003). Measuring inconsistency in meta-analyses. *British Medical Journal, 327*(7414), 557–560. https://doi.org/10.1136/bmj.327.7414.557

Hinchliff, C. E., Smith, S. A., Allman, J. F., Burleigh, J. G., Chaudhary, R., Coghill, L. M., Crandall, K. A., Deng, J., Drew, B. T., Gazis, R., Gude, K., Hibbett, D. S., Katz, L. A., Laughinghouse, H. D., McTavish, E. J., Midford, P. E., Owen, C. L., Ree, R. H., Rees, J. A., … Cranston, K. A. (2015). Synthesis of phylogeny and taxonomy into a comprehensive tree of life. *Proceedings of the National Academy of Sciences, 112*(41), 12764–12769. https://doi.org/10.1073/pnas.1423041112

Jennings, D. J., Boys, R. J., & Gammell, M. P. (2017). Weapon damage is associated with contest dynamics but not mating success in fallow deer (*Dama dama*). *Biology Letters, 13*(11), Article 20170565. https://doi.org/10.1098/rsbl.2017.0565

Jin, J. J. H., & Shipman, P. (2010). Documenting natural wear on antlers: A first step in identifying use-wear on purported antler tools. *Quaternary International, 211*(1), 91–102. https://doi.org/10.1016/j.quaint.2009.06.023

Johns, A., Gotoh, H., McCullough, E. L., Emlen, D. J., & Lavine, L. C. (2014). Heightened condition-dependent growth of sexually selected weapons in the rhinoceros beetle, *Trypoxylus dichotomus* (Coleoptera: Scarabaeidae). *Integrative and Comparative Biology, 54*(4), 614–621. https://doi.org/10.1093/icb/icu041

Johnson, H. E., Bleich, V. C., & Krausman, P. R. (2005). Antler breakage in tule elk, Owens Valley, California. *Journal of Wildlife Management, 69*(4), 1747–1752. https://doi.org/10.2193/0022-541X(2005)69[1747:ABITEO]2.0.CO;2

Johnson, H. E., Bleich, V. C., & Krausman, P. R. (2007a). Mineral deficiencies in tule elk, Owens Valley, California. *Journal of Wildlife Diseases, 43*(1), 61–74. https://doi.org/10.7589/0090-3558-43.1.61

Johnson, H. E., Bleich, V. C., Krausman, P. R., & Koprowski, J. L. (2007b). Effects of antler breakage on mating behavior in male tule elk (*Cervus elaphus nannodes*). *European Journal of Wildlife Research, 53*(1), 9–15. https://doi.org/10.1007/s10344-006-0060-4

Jones, A. R. (1980). Chela injuries in the fiddler crab, *Uca burgersi* Holthuis. *Marine Behavior & Physiology, 7*(1), 47–56. https://doi.org/10.1080/10236248009386970

Jones, P. D., Strickland, B. K., Demarais, S., Wang, G., & Dacus, C. M. (2018). Nutrition and ontogeny influence weapon development in a long-lived mammal. *Canadian Journal of Zoology, 96*(9), 955–962. https://doi.org/10.1139/cjz-2017-0345

Judge, K. A., & Bonanno, V. L. (2008). Male weaponry in a fighting cricket. *PLoS One, 3*(12), Article e3980. https://doi.org/10.1371/journal.pone.0003980

Karns, G. R., & Ditchkoff, S. S. (2012). Antler breakage patterns in white-tailed deer. *Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies, 66*, 114–119.

Kimock, C. M., Brent, L. J., Dubuc, C., & Higham, J. P. (2022). Body size and canine size do not confer a competitive advantage in male rhesus macaques. *Animal Behaviour, 187*, 281–290. https://doi.org/10.1016/j.anbehav.2022.01.011

Kitchener, A. (1991). The evolution and mechanical design of horns and antlers. In J. M. V. Rayner, & R. J. Wootton (Eds.), *Biomechanics in evolution* (pp. 229–253). Cambridge University Press.

Kochensparger, S. K., Painting, C. J., Buzatto, B. A., & McCullough, E. L. (2024). Are weapon allometries steeper in major or minor males? A meta-analysis. *Behavioral Ecology*. https://doi.org/10.1093/beheco/arae069. arae069.

Kojima, W., & Lin, C.-P. (2017). It takes two to tango: Functional roles, sexual selection and allometry of multiple male weapons in the flower beetle *Dicronocephalus wallichii bourgoini*. *Biological Journal of the Linnean Society, 121*(3), 514–529. https://doi.org/10.1093/biolinnean/blx018

Koricheva, J., Gurevitch, J., & Mengersen, K. (2013). *Handbook of meta-analysis in ecology and evolution*. Princeton University Press.

Lailvaux, S. P., Reaney, L. T., & Backwell, P. R. Y. (2009). Dishonest signalling of fighting ability and multiple performance traits in the fiddler crab *Uca mjoebergi*. *Functional Ecology, 23*(2), 359–366. https://doi.org/10.1111/j.1365-2435.2008.01501.x

Landete-Castillejos, T., Currey, J. D., Estevez, J. A., Fierro, Y., Calatayud, A., Ceacero, F., Garcia, A. J., & Gallego, L. (2010). Do drastic weather effects on diet influence changes in chemical composition, mechanical properties and structure in deer antlers? *Bone, 47*(4), 815–825. https://doi.org/10.1016/j.bone.2010.07.021

Lane, S. M., & Briffa, M. (2017). The price of attack: Rethinking damage costs in animal contests. *Animal Behaviour, 126*, 23–29. https://doi.org/10.1016/j.anbehav.2017.01.015

Lincoln, G. A. (1972). The role of antlers in the behaviour of red deer. *Journal of Experimental Zoology, 182*(2), 233–249. https://doi.org/10.1002/jez.1401820208

Lincoln, G. A. (1992). Biology of antlers. *Journal of Zoology, 226*(3), 517–528. https://doi.org/10.1111/j.1469-7998.1992.tb07495.x

Longair, R. W. (2004). Tusked males, male dimorphism and nesting behavior in a subsocial afrotropical wasp, *Synagris cornuta*, and weapons and dimorphism in the genus (Hymenoptera: Vespidae: Eumeninae). *Journal of the Kansas Entomological Society, 77*(4), 528–557. https://doi.org/10.2317/e-38.1

Lovari, S., Pellizzi, B., Boesi, R., & Fusani, L. (2009). Mating dominance amongst male Himalayan tahr: Blonds do better. *Behavioural Processes, 81*(1), 20–25. https://doi.org/10.1016/j.beproc.2008.12.008

Madewell, R., & Moczek, A. P. (2006). Horn possession reduces maneuverability in the horn-polyphenic beetle, *Onthophagus nigriventris*. *Journal of Insect Science, 6*(1), 21. https://doi.org/10.1673/2006_06_21.1

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

McCullough, E. L., Ledger, K. J., & Moore, T. Y. (2015a). Variation in cross-sectional horn shape within and among rhinoceros beetle species. *Biological Journal of the Linnean Society, 115*, 810—817. https://doi.org/10.1111/bij.12557

McCullough, E. L., Ledger, K. J., O'Brien, D. M., & Emlen, D. J. (2015b). Variation in the allometry of exaggerated rhinoceros beetle horns. *Animal Behaviour, 109*, 133—140. https://doi.org/10.1016/j.anbehav.2015.08.013

McCullough, E. L., Miller, C. W., & Emlen, D. J. (2016). Why sexually selected ornaments are not weapons. *Trends in Ecology & Evolution, 31*, 742—751. https://doi.org/10.1016/j.tree.2016.07.004

McCullough, E. L., & O'Brien, D. M. (2022). Variation in allometry along the weapon-signal continuum. *Evolutionary Ecology, 36*(4), 591—604. https://doi.org/10.1007/s10682-022-10158-9

McCullough, E. L., Tobalske, B. W., & Emlen, D. J. (2014). Structural adaptations to diverse fighting styles in sexually selected weapons. *Proceedings of the National Academy of Sciences, 111*(40), 14484—14488. https://doi.org/10.1073/pnas.1409585111

McEvoy, I., Daniels, L., & Emberts, Z. (2024). Sexually selected weapons can wear out, decreasing their effectiveness in combat. *Proceedings of the Royal Society B: Biological Sciences, 291*(2027), Article 20241090. https://doi.org/10.1098/rspb.2024.1090

McLain, D. K., McBrayer, L. D., Pratt, A. E., & Moore, S. (2010). Performance capacity of fiddler crab males with regenerated versus original claws and success by claw type in territorial contests. *Ethology Ecology & Evolution, 22*(1), 37—49. https://doi.org/10.1080/03949370903515950

Mellon, D. (1999). Muscle restructuring in crustaceans: Myofiber death, transfiguration and rebirth. *American Zoologist, 39*(3), 527—540. https://doi.org/10.1093/icb/39.3.527

Michonneau, F., Brown, J. W., & Winter, D. J. (2016). rotl: An R package to interact with the Open Tree of Life data. *Methods in Ecology and Evolution, 7*(12), 1476—1481. https://doi.org/10.1111/2041-210x.12593

Moen, R. A., Pastor, J., & Cohen, Y. (1999). Antler growth and extinction of Irish elk. *Evolutionary Ecology Research, 1*(2), 235—249.

Muramatsu, D., & Koga, T. (2016). Fighting with an unreliable weapon: Opponent choice and risk avoidance in fiddler crab contests. *Behavioral Ecology and Sociobiology, 70*(5), 713—724. https://doi.org/10.1007/s00265-016-2094-2

Nakagawa, S., & Santos, E. S. A. (2012). Methodological issues and advances in biological meta-analysis. *Evolutionary Ecology, 26*(5), 1253—1274. https://doi.org/10.1007/s10682-012-9555-5

Nweeia, M. T., Eichmiller, F. C., Hauschka, P. V., Donahue, G. A., Orr, J. R., Ferguson, S. H., Watt, C. A., Mead, J. G., Potter, C. W., & Dietz, R. (2014). Sensory ability in the narwhal tooth organ system. *Anatomical Record, 297*(4), 599—617. https://doi.org/10.1002/ar.22886

O'Brien, D. M., Allen, C. E., Van Kleeck, M. J., Hone, D., Knell, R., Knapp, A., Christiansen, S., & Emlen, D. J. (2018). On the evolution of extreme structures: Static scaling and the function of sexually selected signals. *Animal Behaviour, 144*, 95—108. https://doi.org/10.1016/j.anbehav.2018.08.005

O'Dea, R. E., Lagisz, M., Jennions, M. D., Koricheva, J., Noble, D. W. A., Parker, T. H., Gurevitch, J., Page, M. J., Stewart, G., Moher, D., & Nakagawa, S. (2021). Preferred reporting items for systematic reviews and meta-analyses in ecology and evolutionary biology: A PRISMA extension. *Biological Reviews, 96*(5), 1695—1722. https://doi.org/10.1111/brv.12721

Packer, C. (1979). Male dominance and reproductive activity in *Papio anubis*. *Animal Behaviour, 27*, 37—45. https://doi.org/10.1016/0003-3472(79)90127-1

Packer, C. (1983). Sexual dimorphism: The horns of African antelopes. *Science, 221*(4616), 1191—1193. https://doi.org/10.1126/science.221.4616.1191

Painting, C. J., & Holwell, G. I. (2013). Exaggerated trait allometry, compensation and trade-offs in the New Zealand giraffe weevil (*Lasiorhynchus barbicornis*). *PLoS One, 8*(11), Article e82467. https://doi.org/10.1371/journal.pone.0082467

Palaoro, A. V., & Peixoto, P. E. C. (2022). The hidden links between animal weapons, fighting style, and their effect on contest success: A meta-analysis. *Biological Reviews, 97*(5), 1948—1966. https://doi.org/10.1111/brv.12877

Palaoro, A. V., Peixoto, P. E. C., Benso-Lopes, F., Boligon, D. S., & Santos, S. (2020). Fight intensity correlates with stronger and more mechanically efficient weapons in three species of *Aegla* crabs. *Behavioral Ecology and Sociobiology, 74*(5), 53. https://doi.org/10.1007/s00265-020-02834-z

Palmer, A. R., Taylor, G. M., & Barton, A. (1999). Cuticle strength and the size-dependence of safety factors in *Cancer* crab claws. *Biological Bulletin, 196*(3), 281—294. https://doi.org/10.2307/1542953

Paradis, E., Claude, J., & Strimmer, K. (2004). APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics, 20*(2), 289—290. https://doi.org/10.1093/bioinformatics/btg412

Payne, R. J. H. (1998). Gradually escalating fights and displays: The cumulative assessment model. *Animal Behaviour, 56*(3), 651—662. https://doi.org/10.1006/anbe.1998.0835

Pei, K. (1996). Post-natal growth of the formosan reeves' muntjac *Muntiacus reevesi micrurus*. *Zoological Studies, 35*(2), 111—117.

Pereira, A., Tracey, E., Cooney, P. C., Korey, C. A., & Hughes, M. (2014). Post-autotomy claw regrowth and functional recovery in the snapping shrimp *Alpheus angulosus*. *Marine and Freshwater Behaviour and Physiology, 47*(3), 147—159. https://doi.org/10.1080/10236244.2014.928460

Picavet, P. P., & Balligand, M. (2016). Organic and mechanical properties of cervidae antlers: A review. *Veterinary Research Communications, 40*(3), 141—147. https://doi.org/10.1007/s11259-016-9663-8

Porsild, M. P. (1922). Scattered observations on narwhals. *Journal of Mammalogy, 3*(1), 8—13. https://doi.org/10.2307/1373444

Rico-Guevara, A., & Araya-Salas, M. (2015). Bills as daggers? A test for sexually dimorphic weapons in a lekking hummingbird. *Behavioral Ecology, 26*(1), 21—29. https://doi.org/10.1093/beheco/aru182

Rico-Guevara, A., & Hurme, K. J. (2019). Intrasexually selected weapons. *Biological Reviews, 94*(1), 60—101. https://doi.org/10.1111/brv.12436

Rojas, R., Morales, M. C., Rivadeneira, M. M., & Thiel, M. (2012). Male morphotypes in the Andean river shrimp *Cryphiops caementarius* (Decapoda: Caridea): Morphology, coloration and injuries. *Journal of Zoology, 288*(1), 21—32. https://doi.org/10.1111/j.1469-7998.2012.00922.x

Silverman, H. B., & Dunbar, M. J. (1980). Aggressive tusk use by the narwhal (*Monodon monoceros* L.). *Nature, 284*(5751), 57—58. https://doi.org/10.1038/284057a0

Simmons, L. W., & Emlen, D. J. (2006). Evolutionary trade-off between weapons and testes. *Proceedings of the National Academy of Sciences, 103*(44), 16346—16351. https://doi.org/10.1073/pnas.0603474103

Siva-Jothy, M. (1987). Mate securing tactics and the cost of fighting in the Japanese horned beetle, *Allomyrina dichotoma* L. (Scarabaeidae). *Journal of Ethology, 5*(2), 165—172. https://doi.org/10.1007/BF02349949

Somjee, U., Woods, H. A., Duell, M., & Miller, C. W. (2018). The hidden cost of sexually selected traits: The metabolic expense of maintaining a sexually selected weapon. *Proceedings of the Royal Society B: Biological Sciences, 285*(1891), Article 20181685. https://doi.org/10.1098/rspb.2018.1685

Swanson, B. O., George, M. N., Anderson, S. P., & Christy, J. H. (2013). Evolutionary variation in the mechanics of fiddler crab claws. *BMC Evolutionary Biology, 13*(1), 1—11. https://doi.org/10.1186/1471-2148-13-137

Tina, F. W., & Keeratipattarakarn, K. (2019). Winning status of regenerated-clawed males in contests with original-clawed males in *Austruca perplexa* (Brachyura, Ocypodidae). *Crustaceana, 92*(3), 373—383. https://doi.org/10.1163/15685403-00003885

Tullis, A., & Straube, C. H. T. (2017). The metabolic cost of carrying a sexually selected trait in the male fiddler crab *Uca pugilator*. *Journal of Experimental Biology, 220*(20), 3641. https://doi.org/10.1242/jeb.163816

Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor Package. *Journal of Statistical Software, 36*(3), 1—48. https://doi.org/10.18637/jss.v036.i03

Wainwright, S. A., Biggs, W. D., Currey, J. D., & Gosline, J. M. (1976). *Mechanical design in organisms*. Princeton University Press.

Wang, N. (2023). Conducting meta-analyses of proportions in R. *Journal of Behavioral Data Science, 3*(2), 64—126. https://doi.org/10.35566/jbds/v3n2/wang

Woodman, T. E., Chen, S., Emberts, Z., Wilner, D., Federle, W., & Miller, C. W. (2021). Developmental nutrition affects the structural integrity of a sexually selected weapon. *Integrative and Comparative Biology, 61*(2), 723—735. https://doi.org/10.1093/icb/icab130

Zhao, A., Qin, H., & Fu, X. (2016). What determines the regenerative capacity in animals? *BioScience, 66*(9), 735—746. https://doi.org/10.1093/biosci/biw079