Opinion

# Towards an integrated understanding of animal weapons


Authors:

1. **Christine W. Miller**, Department of Zoology, University of Cambridge, UK, ORCID: 0000-0003-1359-5624, cwm30@cam.ac.uk
2. **Dominic Cram**, University of East Anglia, UK, ORCID: 0000-0002-8790-8294, d.cram@uea.ac.uk
3. **Sarah M. Lane**, School of Biological and Marine Sciences, University of Plymouth, UK ORCID: 0000-0002-3797-3178, sarah.lane@plymouth.ac.uk
4. **#Romain Boisseau**, Department of Ecology & Evolution, University of Lausanne, Switzerland, ORCID: 0000-0003-4317-1064, romain.boisseau@unil.ch
5. **#Sophia Fitzgerald**, Division of Biological Sciences, University of Montana, USA, ORCID: 0009-0007-6776-4856, sophia.fitzgerald@umconnect.umt.edu
6. **#Nicole Lopez**, Division of Biological Sciences, University of Montana, USA, 0000-0002-6579-7765, nicole1.lopez@umconnect.umt.edu
7. **#Allen J. Moore**, Department of Entomology, University of Georgia, USA, ORCID: 0000-0002-1498-3322, ajmoore@uga.edu
8. **#Christina J. Painting**, Te Aka Mātuatua School of Science, University of Waikato, Hamilton, New Zealand, ORCID: 0000-0003-0701-2648, chrissie.painting@waikato.ac.nz
9. **#Alexandre V. Palaoro**, Department of Zoology, Universidade Federal do Paraná (UFPR), Brazil, ORCID: 0000-0002-8629-0728, alexandre.palaoro@gmail.com
10. **#Michael Ryan**, Department of Integrative Biology, University of Texas, USA, ORCID: 0000-0002-6381-9545, mryan@utexas.edu
11. **#Ummat Somjee**, Department of Integrative Biology, University of Texas, USA, ORCID: 0000-0002-5130-3605, ummat.s@gmail.com
12. **#Camille Thomas-Bulle**, Department of Biological Sciences, University of Denver, CO, USA & Department of Ecology & Evolution, University of Lausanne, Switzerland, ORCID: 0000-0002-9042-5066, camille.thomas.bulle@gmail.com
13. **Douglas Emlen**, Division of Biological Sciences, University of Montana, USA, ORCID: 0000-0003-2549-7319, doug.emlen@mso.umt.edu
14. **David Labonte**, Department of Bioengineering, Imperial College London, UK, ORCID: 0000-0002-1952-8732, d.labonte@imperial.ac.uk

# denotes equal contributions

Correspondence: cwm30@cam.ac.uk (C.W. Miller); www.millerlab.net



Keywords: male-male competition, armament, horn, antler, sexual selection

## Abstract

Animals resolve conflict using an astonishing array of weapons – from electric fields and sonic shockwaves to deadly venom and high-impact strikes. Most weapon research has typically considered only a single weapon modality at a time with a focus separately on weapons under sexual selection or natural selection. Further, few studies have examined how weapons are integrated into the larger phenotype. Thus, it is not surprising that major questions remain about why weapons have evolved such extraordinary diversity in form and function. By synthesizing insights across weapon modalities and research traditions, we identify key directions for future research. We propose that animal weapons provide a powerful framework for understanding how conflict drives the evolution of complex, integrated phenotypes.

## Animal weapons provide diverse solutions to conflict

Conflict in nature is not anomalous but rather a central driver of adaptation. **Animal weapons** (see Glossary) have evolved repeatedly to aid in the process of resolving conflict. Weapons are traits that can be used to cause physical harm to others in the process of competing for food and mates, subduing prey, and in self-protection. A single weapon (e.g., the claw of a coconut crab, *Birgus latro*, [1]) may experience natural selection, sexual selection, or both. Weapons are highly diverse and come in multiple modalities [2], including mechanical, chemical, electrical, acoustic, and even thermal weapons (Figure 1). Yet, research on animal weapons has typically focused on one modality at a time and on weapons under similar forms of selection [3-6]. Our objective with this manuscript is to take a more expansive view on animal weapons, with the goal of improving understanding of why nature has come up with such diverse solutions to conflict.

## Mechanical weapons are but one type of weapon

Elegant drawings in the Chauvet-Pont d'Arc Cave in France, dated over 30,000 years before present, depict the horns of woolly rhinoceros (*Coelodonta antiquitatis*), steppe bison (*Bison priscus*), auroch (*Bos primigenius)*, and ibex (*Capra ibex*). Many of us picture such mammalian horns, as well as tusks, spurs, and talons, as quintessential examples of animal weapons. We have typically referred to such weapons as morphological weapons because they are extensions of an animal's morphology. Yet, the term "mechanical weapon" may be more appropriate for two reasons. First, when used as weapons, they deliver force via direct contact with an opponent. Second, all animal weapons are associated to some degree with morphology. For example, chemical weapons, such as venoms, are typically produced by glands. When Asian honeybees "cook" their predators, they use vibrating muscle (Figure 1). Thus, for clarity, we will hereafter refer to weapons as mechanical weapons if they are used directly to deliver force.

Our human visual bias makes it simple to identify mechanical weapons and appreciate their immense diversity [e.g., 3], especially when they are extensions from the body. Unsurprisingly, such weapons have received much attention in theoretical and empirical research. However, mechanical weapons are but one modality of animal weapon (Figure 1). While we mention mechanical, chemical, electrical, acoustic, and thermal weapons here, we do not claim that this list of weapon modalities is complete.

Considering multiple weapon modalities simultaneously is important. Too often in science, traits and phenomena are studied with a narrow focus. In doing so, we lose the opportunity for a broad, coherent and structured understanding of the complexities of living systems. New generalizations and predictive frameworks can emerge when commonalities are recognized and when fields of study are inspired by each other. We next provide an example of how the study of mechanical weapons may benefit from examining the pursuits of those researchers engaged in the study of chemical weapons.

## Mechanical weapon composition, structure, and the ability to weather battle

The composition of chemical weapons is clearly paramount for their effectiveness. For example, cone snails (Genus: *Conus*) hunt fish with a venom containing a mix of multiple paralytic components. Yet, these compounds are insufficient to rapidly immobilize prey; excitotoxins and other compounds must be involved, too. In fact, many species have an entire suite of toxins that act differently in the envenomated fish to increase the likelihood of a successful hunt; at least ~50,000 different conotoxins exist in the *Conus* genus [7,8].

The composition of chemical weapons is often characterized in exquisite detail, with inquiry into the role that each existing compound may play in the weapon's efficacy [9]. In contrast to chemical weapons, mechanical weapons are typically characterized simply by size, general descriptors of shape, and location on the body – rather than directly what makes them effective in physical conflict. Yet, selection on these weapons should be no less intricate in its focus on improved efficacy. Over evolutionary time mechanical weapons are at least occasionally, often frequently, tested in battle [5]. As such, their ability to transfer and withstand forces is a crucial part of their functioning and diversity, and many show the evolutionary hallmarks of generations upon generations of selection via physical combat. For example, antlers of elk (*Cervus canadensis*) are a complex composite and one of the toughest biological materials known [10]. Biomechanical studies examining force, internal architecture, and material composition have only been conducted in a handful of taxa, mostly mammals [10,11,12; Figure 2] and crustaceans [e.g., 13,14,15]. These properties are valuable to understand because they set upper limits on weapon size and can reveal trade-offs between durability, weight, and energetic costs. Just like the composition of chemical weapons, the composition of mechanical weapons can be a less visible aspect of their biodiversity, but undoubtedly it is one of the most important to fitness. While we highlight how the study of mechanical weapon diversity can benefit from the approaches used in the study of chemical weapons, there are undoubtedly many more lessons that can be gained by bringing together perspectives across modalities and fields.

## Weapons function as systems integrated within the phenotype

Regardless of modality, weapons are functionally integrated into the phenotype. For example, the intricate cocktail of venom components would be of little use without a venom-delivery mechanism such as a bite or sting [16]. Weapons typically require numerous **weapon-supportive traits** [17] to be effective. As an illustrative example, bombardier beetles (Genus: Brachinus) squirt a nearly 100°C irritating mixture of benzoquinones from their abdomen, serving as both a thermal and a chemical weapon. This potent weapon relies on glands that produce and store hydrogen peroxide and hydroquinones separately. When the beetle is disturbed, it mixes the contents of the two glands in a heat-resistant chamber in the presence of catalysts. The reaction generates heat and gas, driving the emission. The damage caused can be fatal to attacking insects [18]. In this example, the morphological glands, the chemical catalysts, and the behavior of directing the emission all serve as weapon-supportive traits.

During the mating season, the crashing of male bighorn sheep (*Ovis canadensis*) can be heard echoing throughout canyons in North America. Males rear up and deliver blows with an impact force more than five times the load required to crack a human skull. The horns of bighorn sheep would be of little use without combat behaviors, as well as a suite of anatomical and physiological modifications throughout the body that serve as weapon-supportive traits (Figure 2; [19]).

Weapons and their supportive traits together comprise **weapon systems.** Weapon systems are integrated suites of traits, and they are likely to show similarities to other phenotypically integrated systems. For example, petal size, shape, color, nectar production, and stamen/pistil length can be tightly correlated in flowering plants. These traits are genetically and functionally linked because they collectively affect how well specific pollinators can access and transfer pollen. Selection acts on the whole trait complex, not each trait independently [20]. To study phenotypic integration of weapon systems, we can adopt approaches used in flowering plants and other studies of phenotypic integration. Work in this area should measure multiple components of the weapon system, analyzing how selection influences trait covariation and integration. Some weapons serve a myriad of functions, while others serve few. How weapon multifunctionality influences their integration is largely unknown.

## Weapons are multifunctional

Multifunctionality in animal weapons may be more rule than exception. Consider the following examples: the canine teeth of wolves, *Canis lupus,* are used as an informative signal to conspecifics, in same-sex physical combat, to subdue prey, to shear meat off bones during feeding, and in carcass defense against heterospecifics [21,22]; the enlarged mandibles of the male Auckland tree wētā, *Hemideima thoracica,* are used in fights over females and in foraging [23]; cnidarian sea anemones (Order: Actiniaria) have evolved a versatile venom system that is used to hunt, to engage in conspecific territorial disputes, and for defense [24]. As these examples illustrate, traits can serve as **sexually selected weapons** while still being used for other functions. A single weapon can experience selection from numerous sources; it is the result of a summation of evolutionary forces that may be in opposition or may be somewhat aligned. Thus, we may expect that a body part serving very different functions (such as a leg used for locomotion as well as for fighting [25]) may have lower phenotypic integration across its system of supportive traits relative to those weapons with fewer or more aligned functions (such as use in hunting prey and attacking conspecifics [see, e.g., 26]).

## Behavior may take the lead in weapon elaboration and diversification

Many weapons would be ineffective without their suite of weapon-supportive traits, including specialized behaviors. Conversely, many behavioral examples of physical conflict exist without obvious weapon elaboration [27]. For example, the common bottlenose dolphin, *Tursiops truncatus*, uses ramming, scraping with nonexaggerated teeth, body slaps, and endurance [28]. Ring doves, *Streptopelia risori*, engage in wing slapping and chest bumping [29]. *Drosophila melanogaster* fruit flies tap or push each other using their forelegs [30]. In these cases, animal bodies show no obvious signs of anatomical modification. Such examples highlight that behavior may take the lead in the initial elaboration of animal weapons by shaping the selective environments that individuals experience [see, e.g., 31,32].

Once a weapon begins to take form, behavior likely contributes to further evolutionary diversification. For example, African antelope (Family: Bovidae) exhibit spectacular horn diversity across species. This evolutionary diversification is likely at least partially due to differences in fighting style and signaling across habitat types. Open habitats are hypothesized to have selected for large, lateral weapons that are visible to rivals from long distances. Such habitat allows space for fighting with large weapons, because the animals have room to maneuver. In contrast, smaller, forward-facing weapons are expected to have evolved in closed habitats where wide horns would get tangled and where the reliance on weapons as signals is reduced [33,34].

Changes in habitat and the fighting environment may stimulate large changes in how animals engage in conflict. However, individuals within a species and in a single context often exhibit differences in how they engage in competitive or agonistic interactions [35]. Some individuals will direct and wield weapons more effectively (i.e., more skillfully) in a certain context than will others, and it is largely unknown the degree to which skill plays a role in contest success [36]. We also do not know how skills are acquired. Do skillful parents produce skillful offspring? Are skills refined, for example, through battle experience or juvenile play behavior? Foraging skills can be socially learned, allowing innovations to rapidly spread through populations [37], but whether the same applies to fighting skills remains unclear.

## Weapons as signals and consequences for diversification

One of the functions of many weapons is their use as signals of vigor, fighting ability, or agonistic intention. For example, males of the red deer, *Cervus elaphus*, display their antlers as they walk in parallel to each other, their behavior facilitating visual assessment [38]. Signaling can help minimize the costs and risks of contests by allowing an evaluation of probable outcomes, which can halt physical conflict before further escalation [39,40]. When a weapon is used as a signal, this process can contribute to weapon diversification. We describe three ways this can occur.

First, selection via signaling can lead to the evolution of different weapon features than selection via physical conflict alone. For example, long fiddler crab claws are effective visual signals to opponents, but long claw length is not helpful for fighting. Males deliver gripping forces not at the tips of the claws but closer to the body at the tubercles. Thus, the claw shape of fiddler crabs is molded by selection to serve both as an effective signal and to be successful in fighting, which may result in some compromises [41]. Second, another way that signaling can lead to the elaboration and diversification of weapons is via runaway evolution via intra-sexual sexual selection, which requires signals to be reliable and honest [42]. Unreliable or dishonest signals may eventually arise [40] and are expected to put the brakes on this process. Third, for a weapon to serve as a signal, it must be perceived. Yet, perception is rarely perfect. We know very little about the sensory and cognitive underpinnings involved in the assessment of weapons by rivals [see 43]. In some cases, there may be a disconnect between the information perceptually gleaned from the signal and the weapon's true effectiveness in battle [e.g., 44,45]. For example, the ambient environmental conditions experienced by some populations, such as the amount of or quality of light filtering through a canopy of vegetation, may affect visual perception [43,46]. Further, accurate discrimination may require larger relative differences in weapon sizes for weapons that are absolutely larger [Weber's Law; 47]. Altogether, it is probable that assessment will sometimes be faulty, and this can serve as another factor influencing weapon diversification.

## Costs and constraints have consequences for weapon diversification

The benefit of possessing weapons is often apparent in this conflict-filled world. Thus, it can seem surprising when animals lose or reduce weapons or over evolutionary time [48]. Phylogenetic comparative analyses have shown that weapons are highly labile over evolutionary time; they can increase in size and complexity, yet equally-so, they may readily disappear [25,48,49]. To fully understand weapon diversification, it is essential to consider why weapons, with all their advantages, may become reduced or even lost over evolutionary time.

Venom, for example, is a dynamically evolving weapon; the loss of genetic capacity to produce certain component toxins is surprisingly common [e.g., 9,50]. Venom is a multi-component, functional trait used by one organism to interfere with the homeostatic processes of another, generally to facilitate feeding or deter predators or competitors. The composition of venom actively coevolves with the physiology of prey animals in a coevolutionary arms race. As prey become resistant, there may be strong selection for novel components with greater efficacy. Components that are less effective, in turn, are expected to be lost if there is a cost to their production, maintenance, and/or storage [51].

Weapons, especially sexually selected weapons, can be associated with steep costs [52,53] and sexually antagonistic effects [54]. The weapon cost-benefit relationship may be altered by biotic and abiotic environmental change, such as resource defensibility, habitat structure, temperature stress, or parasite load – and all of these can vary readily across space and time. In some such contexts, costs of weapons may exceed benefits. When they do, natural selection may reverse or slow weapon elaboration.

Weapon reduction or loss is not necessarily the only outcome when weapons are costly. Instead, selection may lead to the evolution of **weapon compensatory traits** [55-57]. Weapon compensatory traits can be distinguished from supportive traits in that they alleviate costs that are not directly linked to effective weapon deployment, such as the energetic costs of walking or flying with large horns or mandibles. Compensation may manifest as novel or modified structures, physiology, behavior, or performance [55]. For example, electric eels, Genus *Electrophorus,* can generate large electrical discharges – up to 600 volts – without injuring themselves [58]. The ability to avoid self-electrocution is hypothesized to be due to compensatory traits including the ability to control and channel electricity. These traits include the separation and insulation of electric organs and the ability to reduce current flow within the body.

Weapon diversification is not only shaped by costs; it can also be shaped by constraints such as those arising from phylogeny, architecture, and development [59]. Such constraints may at least partially explain why some taxa have evolved chemical instead of acoustic weapons, and why weapons are found only on some locations on the body. Biomechanical constraints may help explain why the evolution of weapons in highly flight-dependent species is limited. For example, specialized weapons are rare in bird species that rely upon efficient flight as their main form of locomotion [60]. Further, even though male damselflies (Suborder: Zygoptera) and butterflies (Superfamily: Papilionoidea) compete for territories, they do so while lacking obvious weapons [61,62]. Instead, such animals, as well as the dolphin, dove, and fruit fly mentioned earlier, engage in conflict with wings, beaks, teeth, and tails that may show little indication of being modified for fighting.

## Concluding Remarks

Conflict is rife in nature, and animal weapons showcase highly diverse solutions to conflict. Yet research has traditionally focused on a narrow subset of highly visible mechanical traits, often studied in isolation and under similar selective contexts. By adopting a broader perspective that integrates multiple weapon modalities, we argue that animal weapons are best understood as distinct evolutionary solutions to conflict that nonetheless share common underlying principles (see **Outstanding Questions**). Across modalities, weapons are shaped by selection on performance, embedded within integrated phenotypic systems, and constrained by costs, trade-offs, and limits imposed by development, biomechanics, and perception.

A key insight emerging from this synthesis is that weapons do not evolve alone. Their efficacy and elaboration depend on suites of weapon-supportive and compensatory traits, including behavior and skill, which may precede, facilitate, or constrain morphological elaboration. Moreover, the widespread multifunctionality of weapons means that their evolution reflects the cumulative outcome of often competing selective pressures, rather than optimization for any single function. These dynamics may help explain both the extraordinary diversity of animal weapons and their striking evolutionary lability, including repeated reduction and loss.

Future progress will be enhanced by the use of experimental and comparative approaches that bridge research traditions. Integrating biomechanics, physiology, behavior, and phylogenetics and considering multiple weapon modalities will allow researchers to move beyond descriptive classifications toward broadly predictive frameworks for weapon evolution. Such approaches promise not only to clarify why particular weapon types evolve in some lineages and not others, but also to illuminate general principles of phenotypic integration, adaptation, and diversification. In this way, animal weapons provide a powerful lens through which to understand how conflict shapes the evolution of complex biological systems.

## Boxes

### Glossary

Animal Weapon: A weapon is a trait that can be used to cause physical harm to others in the context of competitive or agonistic interactions

Sexually selected weapon: A weapon can be described as sexually selected if variation in its expression has led to fitness differences associated with non-random success in the competition for access to gametes for fertilization (based on [63])

Weapon compensatory trait: Weapon compensatory traits mitigate the costs associated with the development, use, or maintenance of weapons

Weapon-supportive trait: Weapon-supportive traits enable weapon function and improve their effectiveness.

Weapon system: Weapon systems include one or more animal weapons alongside their array of weapon-supportive traits

## Declaration of interests

The authors declare no competing interests.

## Acknowledgments

We used the Delphi technique (Supplementary Information), to generate ideas and decide on the areas of focus for this manuscript. This work was inspired by work funded by the US National Science Foundation (IOS-2226881) to C.W.M. Thanks also to Janice Yan for providing comments on a previous version.

## References

1. Oka, S.-i. et al. (2016) A mighty claw: pinching force of the coconut crab, the largest terrestrial crustacean. *PLoS ONE* 11, e0166108
2. Lane, S.M. (2018) What is a weapon? *Integr. Comp. Biol.* 58, 1055–1063
3. Emlen, D.J. (2008) The evolution of animal weapons. *Annu. Rev. Ecol. Evol. Syst.* 39, 387–413
4. Geist, V. (1966) The evolution of horn-like organs. *Behaviour* 26, 175–214
5. McCullough, E.L. et al. (2016) Why sexually selected weapons are not ornaments. *Trends Ecol. Evol.* 31, 742–751
6. Palaoro, A.V. and Peixoto, P.E.C. (2022) The hidden links between animal weapons, fighting style, and their effect on contest success: a meta-analysis. *Biol. Rev.* 97, 1948–1966
7. Olivera, B.M. and Cruz, L.J. (2001) Conotoxins, in retrospect. *Toxicon* 39, 7–14
8. Terlau, H. et al. (1996) Strategy for rapid immobilization of prey by a fish-hunting marine snail. *Nature* 381, 148–151
9. Dowell, N.L. et al. (2016) The deep origin and recent loss of venom toxin genes in rattlesnakes. *Curr. Biol.* 26, 2434–2445
10. Launey, M.E. et al. (2010) Mechanistic aspects of the fracture toughness of elk antler bone. *Acta Biomater.* 6, 1505–1514
11. Kitchener, A.C. (2021) Fighting and the mechanical design of horns and antlers. In *Biomechanics in Animal Behaviour* (A.C. Kitchener, ed.), pp. 291–314, Garland Science
12. Wheatley, B.B. et al. (2023) How the geometry and mechanics of bighorn sheep horns mitigate the effects of impact and reduce the head injury criterion. *Bioinspir. Biomim.* 18, 026005
13. Swanson, B.O. et al. (2013) Evolutionary variation in the mechanics of fiddler crab claws. *BMC Evol. Biol.* 13, 137
14. Qian, Z. et al. (2018) Structure, mechanical properties and surface morphology of the snapping shrimp claw. *J. Mater. Sci.* 53, 10666–10678
15. Patek, S.N. and Caldwell, R.L. (2005) Extreme impact and cavitation forces of a biological hammer: strike forces of the peacock mantis shrimp *Odontodactylus scyllarus*. *J. Exp. Biol.* 208, 3655–3664

16. Jenner, R.A. et al. (2025) What is animal venom? Rethinking a manipulative weapon. *Trends Ecol. Evol.* 40, 852-861
17. Okada, Y. et al. (2012) Effect of weapon-supportive traits on fighting success in armed insects. *Anim. Behav.* 83, 1001–1006
18. Eisner, T. and Aneshansley, D.J. (1999) Spray aiming in the bombardier beetle: photographic evidence. *Proc. Natl. Acad. Sci. U.S.A.* 96, 9705–9709
19. Kitchener, A.C. (1988) An analysis of the forces of fighting of the blackbuck (*Antilope cervicapra*) and the bighorn sheep (*Ovis canadensis*) and the mechanical design of the horn of bovids. *J. Zool.* 214, 1–20
20. Herrera, C.M. (2001) Deconstructing a floral phenotype: do pollinators select for corolla integration in *Lavandula latifolia*? *J. Evol. Biol.* 14, 574–584
21. Harrington, F.H. et al. (2003) Wolf communication. In *Wolves: Behavior, Ecology, and Conservation* (L.D. Mech and L. Boitani, eds), pp. 66–103, Univ. Chicago Press
22. Tallian, A. et al. (2022) Of wolves and bears: seasonal drivers of interference and exploitation competition between apex predators. *Ecol. Monogr.* 92, e1498
23. Farnworth, B. et al. (2023) Exaggerated mandibles are correlated with enhanced foraging efficacy in male Auckland tree wētā. *Biol. Lett.* 19, 20230207
24. Menezes, C. and Thakur, N.L. (2022) Sea anemone venom: ecological interactions and bioactive potential. *Toxicon* 208, 31–46
25. Miller, C.W. et al. (2024) The evolution of multi-component weapons in leaf-footed bugs. *Evolution* 78, 635–651
26. Rosas-Guerrero, V. et al. (2011) Influence of pollination specialization and breeding system on floral integration and phenotypic variation in *Ipomoea*. *Evolution* 65, 350–364
27. Guo, X. and Dukas, R. (2020) The cost of aggression in an animal without weapons. *Ethology* 126, 24–31
28. Scott, E.M. et al. (2005) Aggression in bottlenose dolphins: evidence for sexual coercion, male–male competition, and female tolerance through analysis of tooth-rake marks and behaviour. *Behaviour* 142, 21–44
29. Vowles, D. and Harwood, D. (1966) The effect of exogenous hormones on aggressive and defensive behaviour in the ring dove (*Streptopelia risoria*). *J. Endocrinol.* 36, 35–51
30. Dierick, H.A. (2007) A method for quantifying aggression in male *Drosophila melanogaster*. *Nat. Protoc.* 2, 2712–2718
31. Duckworth, R.A. (2009) The role of behavior in evolution: a search for mechanism. *Evol. Ecol.* 23, 513–531
32. Wcislo, W.T. (2021) A dual role for behavior in evolution and shaping organismal selective environments. *Annu. Rev. Ecol. Evol. Syst.* 52, 343–362
33. Lundrigan, B. (1996) Morphology of horns and fighting behavior in the family Bovidae. *J. Mammal.* 77, 462–475

34. Bro-Jørgensen, J. (2007) The intensity of sexual selection predicts weapon size in male bovids. *Evolution* 61, 1316–1326
35. Caton, N.R. and Dixson, B.J. (2022) Human third-party observers accurately track fighting skill and vigour along their unique paths to victory. *Sci. Rep.* 12, 14841
36. Briffa, M. and Lane, S.M. (2017) The role of skill in animal contests: a neglected component of fighting ability. *Proc. R. Soc. B* 284, 20171596
37. Aplin, L.M. et al. (2015) Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature* 518, 538–541
38. Clutton-Brock, T.H. et al. (1979) The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus*). *Anim. Behav.* 27, 211–225
39. Smith, J.M. (1974) The theory of games and the evolution of animal conflicts. *J. Theor. Biol.* 47, 209–221
40. Searcy, W.A. and Nowicki, S. (2010) *The Evolution of Animal Communication*. Princeton Univ. Press
41. Dennenmoser, S. and Christy, J.H. (2013) The design of a beautiful weapon: compensation for opposing sexual selection on a trait with two functions. *Evolution* 67, 1181–1188
42. Moore, A.J. et al. (2022) Runaway evolution from male–male competition. *Ecol. Lett.* 25, 295–306
43. Ryan, M.J. and Cummings, M.E. (2013) Perceptual biases and mate choice. *Annu. Rev. Ecol. Evol. Syst.* 44, 437–459
44. Backwell, P.R. et al. (2000) Dishonest signalling in a fiddler crab. *Proc. R. Soc. B* 267, 719–724
45. Caves, E.M. et al. (2018) Categorical perception of colour signals in a songbird. *Nature* 560, 365–367
46. Endler, J.A. (1993) The color of light in forests and its implications. *Ecol. Monogr.* 63, 1–27
47. Akre, K.L. and Johnsen, S. (2014) Psychophysics and the evolution of behavior. *Trends Ecol. Evol.* 29, 291–300
48. Wiens, J.J. (2001) Widespread loss of sexually selected traits: how the peacock lost its spots. *Trends Ecol. Evol.* 16, 517–523
49. Van Kleeck-Hann, M. and Wiens, J.J. (2023) Macroevolution of sexually selected weapons in chameleons. *Evolution* 77, 2277–2290
50. Surm, J.M. et al. (2024) Venom trade-off shapes interspecific interactions, physiology, and reproduction. *Sci. Adv.* 10, eadk3870
51. Evans, E.R. et al. (2019) Venom costs and optimization in scorpions. *Front. Ecol. Evol.* 7, 196
52. Somjee, U. et al. (2018) The hidden cost of sexually selected traits: the metabolic expense of maintaining a sexually selected weapon. *Proc. R. Soc. B* 285, 20181685
53. Joseph, P.N. et al. (2018) Males that drop a sexually selected weapon grow larger testes. *Evolution* 72, 113-122

54. Łukasiewicz, A. et al. (2020) Sexually selected male weapon is associated with lower inbreeding load but higher sex load in the bulb mite. *Evolution* 74, 1851-1855
55. Husak, J.F. and Swallow, J.G. (2011) Compensatory traits and the evolution of male ornaments. *Behaviour* 148, 1–29
56. Oufiero, C. and Garland, T., Jr. (2007) Evaluating performance costs of sexually selected traits. *Funct. Ecol.* 21, 676–689
57. Weber, J.N. et al. (2023) Evolution of horn length and lifting strength in the Japanese rhinoceros beetle *Trypoxylus dichotomus*. *Curr. Biol.* 33, 4285–4297
58. Catania, K.C. (2019) The astonishing behavior of electric eels. *Front. Integr. Neurosci.* 13, 23
59. Gould, S.J. and Lewontin, R.C. (1979) The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proc. R. Soc. B* 205, 581–598
60. Menezes, J.C. and Palaoro, A.V. (2022) Flight hampers the evolution of weapons in birds. *Ecol. Lett.* 25, 624–634
61. Waage, J.K. (1988) Confusion over residency and the escalation of damselfly territorial disputes. *Anim. Behav.* 36, 586–595
62. Kemp, D.J. and Wiklund, C. (2001) Fighting without weaponry: a review of male–male contest competition in butterflies. *Behav. Ecol. Sociobiol.* 49, 429–442
63. Shuker, D.M. and Kvarnemo, C. (2021) The definition of sexual selection. *Behav. Ecol.* 32, 781–794
64. Packer, C. (1979) Male dominance and reproductive activity in *Papio anubis*. *Anim. Behav.* 27, 37–45
65. Schendel, V. et al. (2019) The diversity of venom: the importance of behavior and venom system morphology in understanding its ecology and evolution. *Toxins* 11, 666
66. Kingston, A.C. et al. (2022) Snapping shrimp have helmets that protect their brains by dampening shock waves. *Curr. Biol.* 32, 3576–3583
67. Ono, M. et al. (1995) Unusual thermal defence by a honeybee against mass attack by hornets. *Nature* 377, 334–336
68. Stabentheiner, A. et al. (2007) Thermal behaviour of honeybees during aggressive interactions. *Ethology* 113, 995–1006
69. Huang, W. et al. (2017) Hierarchical structure and compressive deformation mechanisms of bighorn sheep (*Ovis canadensis*) horn. *Acta Biomater.* 64, 1–14
70. Drake, A. et al. (2016) Horn and horn core trabecular bone of bighorn sheep rams absorbs impact energy and reduces brain cavity accelerations during high-impact ramming. *Acta Biomater.* 44, 41–50

## Figure Legends

**Figure 1. Five weapon modalities** (from left to right). *Mechanical weapons* are used to transfer potentially damaging forces via direct physical contact and include structures such as the canines of the olive baboon, *Papio anubis* [64]. *Chemical weapons* are bioactive compounds that can subdue or harm others, and these weapons include venoms [65]. Snails in the genus *Conus* use a small harpoon to transfer a mix of bioactive compounds that subdues prey [8]. *Electrical weapons* include the electrical discharge of electric eels, genus *Electrophorus*. Fascinatingly, this weapon first stimulates prey to move and so reveal itself, and then to freeze, aiding its capture [58]. *Acoustic weapons* include the acoustic shockwaves produced by pistol shrimp and other snapping shrimp in the Family Alpheidae. To employ this weapon, a specialized claw is rapidly shut. The collapse of a cavitation bubble generates an acoustic shockwave with extremely high sound pressure levels, reaching up to 218 decibels [66]. The shockwave can kill and injure both prey and conspecific competitors. *Thermal weapons* include the process by which Japanese honeybees, *Apis cerana japonica*, “cook” their enemy. When a predatory Asian hornet is captured, often more than 500 bees rapidly engulf the hornet in a ball. They vibrate their wing muscles to produce heat, reaching 47 °C, which proves lethal to the hornet but not to the bees [67,68]. Illustrations by A. Whitney Fletcher.

**Figure 2. The weapon system of bighorn sheep (*Ovis canadensis*).** In the cool autumn air in North America, the breath of bighorn sheep is visible as males assess, push, and kick each other. As contests escalate, males rear up on their hindlegs and crash their head into that of their opponent (above) at a speed that can reach 9 m/s. Mechanical weapons, the horns and the skull, provide the primary points of contact,

supporting an impact force up to 3400 N [69] (below). The tapered spiral geometry of the horn and the spongy trabecular bone material within the horn and skull serve to absorb impact [12,70] Weapon-supportive traits may include physiological modifications, such as modulation of hormones and metabolic rate, and adaptations of the sensory system which allow males to evaluate opponents and decide which males to attack. Illustrations by David Tuss.

# Towards an integrated understanding of animal weapons

## Outstanding Questions

**To what degree are evolutionary principles shared across different weapon modalities?**

Comparisons across mechanical, chemical, electrical, acoustic, and thermal weapons is needed to determine to what degree common rules govern performance, costs, and diversification.

**How does selection act on weapons as integrated systems rather than isolated traits?**

Understanding how weapon components, supportive traits, and compensatory traits covary under selection will require multivariate approaches that explicitly measure integration across morphology, physiology, behavior, and performance.

**How does weapon multifunctionality influence evolutionary outcomes?**

Because many weapons serve multiple roles, future research should examine how competing selective pressures shape trade-offs, constrain optimization, and alter phenotypic integration within weapon systems.

**What role does behavior play in initiating and diversifying animal weapons?**

Behavior may precede morphological elaboration by shaping the selective environment experienced during conflict, yet the conditions under which behavior leads or follows weapon evolution remain poorly understood.

**How important are skill, learning, and experience in determining weapon effectiveness?**

Variation in how individuals wield weapons may strongly influence contest outcomes, but fighting skill is rarely quantified. Moreover, the extent to which fighting skill is heritable, learned, or socially transmitted is largely unknown.

**How do constraints shape the distribution of weapon types across taxa?** Phylogenetic, developmental, and biomechanical constraints may limit which weapon modalities can evolve in certain clades, yet these constraints are rarely tested explicitly.

**How does perception influence the evolution of weapons as signals?** Sensory and cognitive limitations may decouple weapon appearance from contest performance, potentially shaping diversification through imperfect assessment.

Figure 1

Figure 2