Opinion

Towards an integrated understanding of animal weapons

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Towards an integrated understanding of animal weapons

Highlights

Animal weapons include such traits as sharp claws, toxic chemical sprays, and immobilizing electric shocks, showcasing highly diverse solutions to conflict. Yet much is unknown about why such diversity has evolved.

Recent research has highlighted that animal weapons do not operate alone; they are often integrated into phenotypes with a wealth of supportive and compensatory traits.

Weapons often serve multiple functions; their evolution reflects the outcome of multivariate selection, rather than optimization for only a single function.

We illustrate how studies of phenotypic integration, multifunctionality, costs, and constraints will both benefit our understanding of weapon evolution and will provide insights valuable to the broader field of evolutionary biology.

Abstract

Animals resolve conflict using an astonishing array of weapons – from electric fields and sonic shockwaves to deadly venom and high-impact strikes. Yet most weapon research has been narrowly focused, for example, only considering mechanical weapons under sexual selection. Further, few studies have examined how weapons are integrated into animal phenotypes. For these reasons 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 themes for future research on animal weapons and discuss several ways in which research into animal weapons can provide broad insights into evolutionary processes.

Animal weapons provide diverse solutions to conflict

Conflict in nature is not anomalous but rather a central driver of adaptation [1]. **Animal weapons** (see Glossary) have evolved repeatedly across taxa 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. Weapons are highly diverse and come in multiple modalities [2], including mechanical, chemical, electrical, acoustic, and even thermal weapons (Figure 1). Despite decades of research on animal weapons, key questions remain about how weapon modality, function, and performance interact with ecology, life history, and developmental constraints to contribute to such extraordinary diversity. One barrier to progress has been that research on animal weapons has typically focused narrowly on one modality at a time and on weapons under similar forms of selection [3-6]. We argue that a more expansive view on animal weapons is needed

Figure 1

to improve 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 expansions or reinforcements 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 Japanese honeybees, *Apis cerana japonica,* "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, especially when they are extensions from the body [e.g., 3]. Unsurprisingly, such weapons have received much attention in theoretical and empirical research. However, mechanical weapons are but one modality of animal weapon (Figure 1).

Considering multiple weapon modalities simultaneously is important. Moreover, the field of evolutionary biology as a whole stands to benefit from research into the wide

Figure 2

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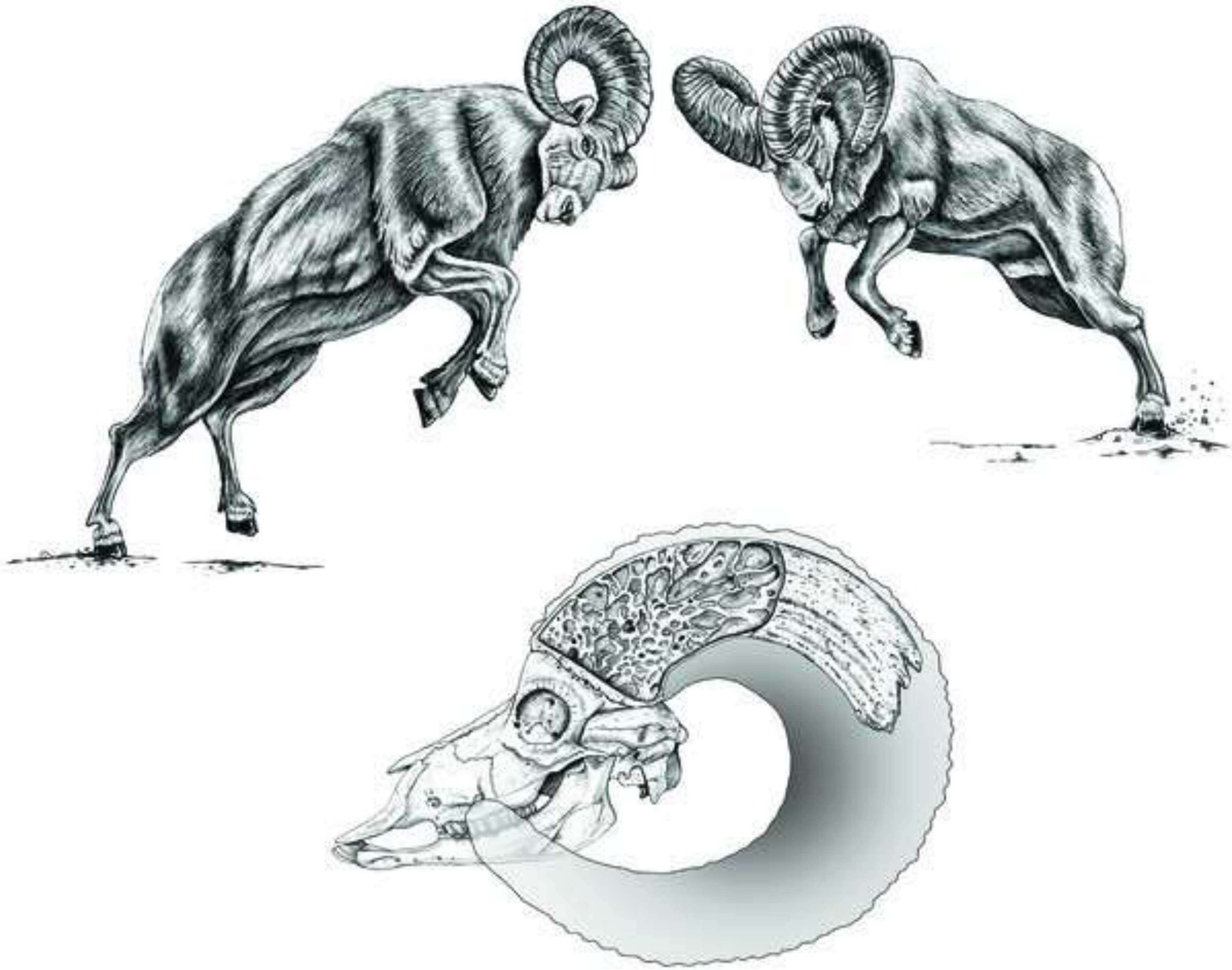


diversity of animal weapons, a topic we discuss later in this article. Too often in science, traits and phenomena are studied with a narrow focus. In doing so, we lose the opportunity for a broad, coherent and structured understanding of the complexities of living systems. New generalizations and predictive frameworks can emerge when commonalities are recognized and when fields of study are inspired by each other [7].

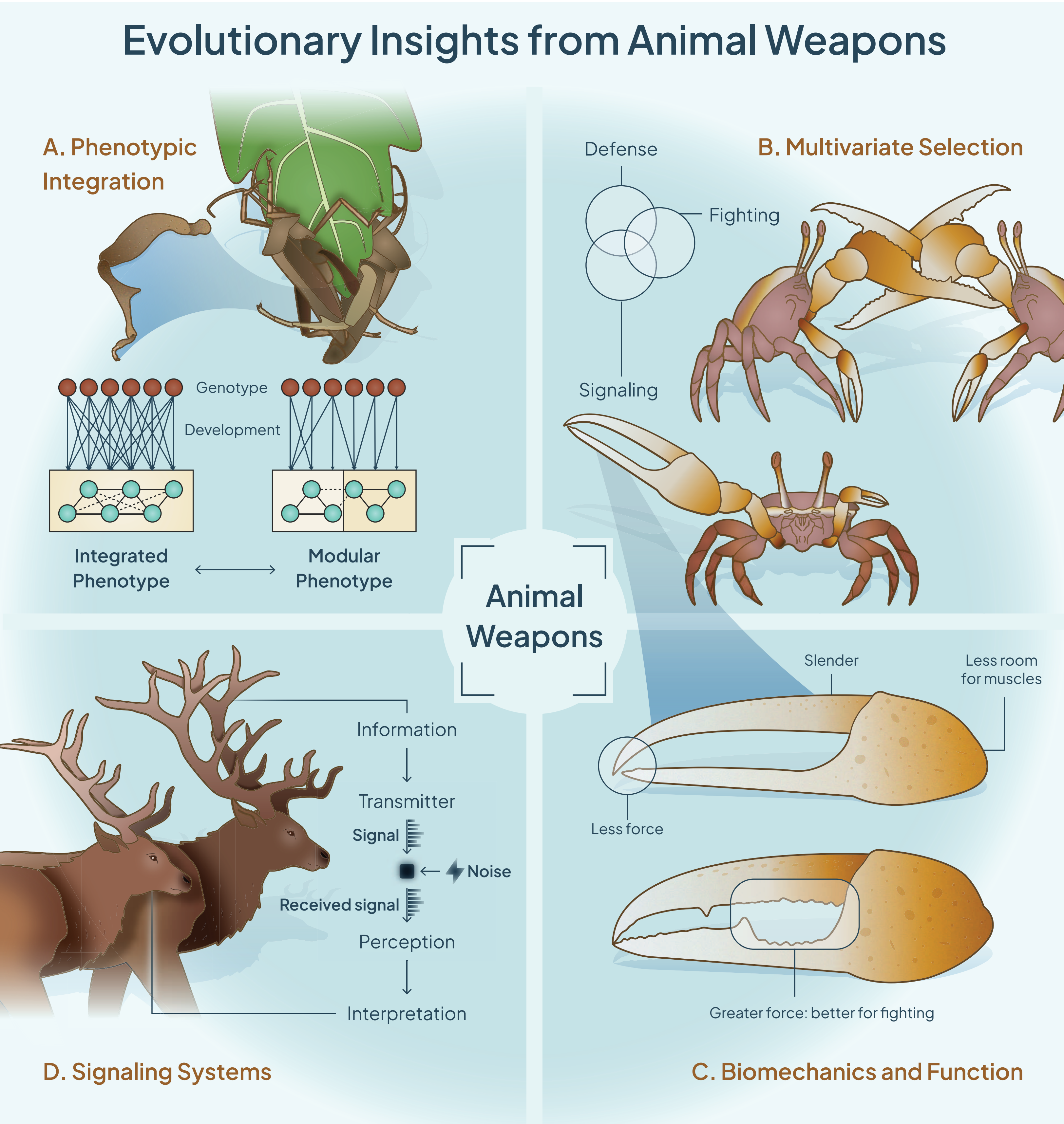
Mechanical weapon composition, structure, and the ability to weather battle

Weapon modalities have been typically studied in isolation, but there is much to gain from a unified perspective. We provide, as an example, how approaches from the study of chemical weapons might benefit those studying mechanical weapons.

The composition of chemical weapons is clearly paramount for their effectiveness. A well-known chemical weapon is **venom**. Cone snails (Genus: *Conus*) provide an example of an animal that uses venom to hunt fish, and their venom contains 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 [8,9].

The composition of chemical weapons is often characterized in exquisite detail, with inquiry into the role that each existing compound plays in the weapon's efficacy [10]. 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 successful in physical conflict. Yet selection on these weapons should be no less intricate and no less potent in improving efficacy. Over

Figure 3


Evolutionary Insights from Animal Weapons
A. Phenotypic Integration
Genotype
Development
Integrated Phenotype
Modular Phenotype
B. Multivariate Selection
Defense
Fighting
Signaling
Animal Weapons
Slender
Less room for muscles
Less force
Greater force: better for fighting
C. Biomechanics and Function
Information
Transmitter
Signal
Noise
Received signal
Perception
Interpretation
D. Signaling Systems

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 one of the toughest biological composites known [10]. Studies examining force, internal architecture, and material composition of mechanical weapons are beginning to gain traction, with focus primarily on mammals [e.g., 11,12,13] (Figure 2) and crustaceans [e.g., 14,15,16] (Figure 3). These properties are valuable to understand broadly because they set upper limits on mechanical 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.

Weapons function as systems integrated within the phenotype

A venom may have a complex chemical composition, but it would be of little use without a venom-delivery mechanism such as a bite or a sting [17]. Weapons of all modalities rely upon weapon supportive traits to be effective [18]. 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 an emission that can be fatal to attacking insects [19]. In this example, the morphological glands, the chemical catalysts, and the behavior of directing the emission all serve as weapon-supportive traits.

Weapon supportive traits are also on clear display in bighorn sheep (*Ovis canadensis*). During the mating season, the crashing of male horn against horn 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 together serve as weapon-supportive traits [11] (Figure 2).

Weapons and their supportive traits together comprise **weapon systems.** Weapon systems should be under strong selection for phenotypic integration, because the coordinated deployment of these systems can be tightly linked to fitness [20]. Phenotypically integrated systems are not rare in the natural world, and studies into weapon integration can both inform and gain from our understanding of other 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. Researchers have found that selection acts on the whole trait complex, not each trait independently [21]. Promising future directions in the study of phenotypic integration in weapon systems include how complex suites of traits are coordinated and how this coordination influences an organism's ability to adapt to new challenges (Figure 2,3).

Weapons are multifunctional

Weapon systems typically act in an integrated fashion, but often the integration must be flexible enough to allow some degree of multifunctionality. Indeed, multifunctionality in animal weapons is more the rule than the exception. Consider the following examples: 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 [22]; 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 [23,24]; many leaf footed bugs (Family: Coreidae) use their hind limbs both for fighting and for locomotion [25], and the enlarged mandibles of the male Auckland tree wētā, *Hemideima thoracica,* are used in fights over females and in foraging [26]. 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 [27]. Resulting dynamics could contribute to both the extraordinary diversity of animal weapons and their striking evolutionary lability, including repeated reduction and loss.

Behavior may take the lead in weapon elaboration and diversification

Interestingly, integrated weapon systems do not always include obvious weapons [28]. For example, fighting in the common bottlenose dolphin, *Tursiops truncatus*, uses ramming, scraping with non-exaggerated teeth, body slaps, and endurance [29]. Ring doves, *Streptopelia risori*, engage in wing slapping and chest bumping [30]. *Drosophila melanogaster* fruit flies tap or push each other using their forelegs [31]. In these cases, animal bodies show no obvious signs of anatomical modification. Such examples highlight that behavior can take the lead in the initial elaboration of animal weapons by shaping the selective environments that individuals experience [see 32,33].

Once a weapon begins to take form, behavior likely contributes to elaboration and 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 that resulted from habitat changes after the last ice age. Open habitats may have resulted in greater long-distance visibility, with this visibility leading to selection for large, lateral weapons that are conspicuous to rivals over long distances. In contrast, closed habitats likely led to smaller, forward-facing weapons where evaluation of a rival would occur over short distances, and where wide horns would get tangled in vegetation [34,35].

Changes in habitat and the fighting environment may stimulate large changes in how animals engage with each other. However, individuals within a species and in a single context also often exhibit differences in combat styles [36]. Some individuals will direct and wield weapons more effectively (i.e., more skillfully) in a certain context than others, yet the role of skill in contest success is largely unknown [37]. 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 skill can be socially learned, allowing innovations to rapidly spread through populations [38], but whether the same applies to fighting skill remains unclear. Future studies should examine if individuals can improve their fighting skill from watching others fight and if first-hand experience leads to more skillful maneuvers.

Weapons as signals and the resulting consequences for diversification

One of the functions of many weapons is their use as signals of vigor, fighting ability, or agonistic intention. 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 evolution and, eventually, diversification. This can occur in three different ways.

First, an honest signal of aggression can generate selection on itself by altering the social environment. This process can cause strong selection and runaway evolution [41]. Second, selection via signaling can lead to the evolution of different weapon features than selection via physical conflict alone (Figure 3) [27]. 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 [42]. In some cases, there will be a disconnect between the information perceptually gleaned from the signal and the weapon's true effectiveness in battle (Figure 3D) [43,44]. For example, ambient environmental conditions, such as the amount or quality of light filtering through a canopy of vegetation, may affect visual perception of individuals [42,45]. Further, accurate interpretation for weapons that are absolutely larger may require greater relative differences in the weapons being assessed [Weber's Law; 46]. We know that in a number of domains, such as foraging, mate choice, mimicry, and predator avoidance (reviewed in [46]) such assessments are based on proportional rather than linear differences; Weber's law predicts that as the absolute size of items being compared increases the proportional differences must be greater to allow discrimination (Just Noticeable Differences). Thus, in agonistic encounters the outcome of physical interactions might be predicted by differences in size on a linear scale while assessment might be based on a proportional scale. It is possible then that perceptual processes might bias individuals in making incorrect decisions about potential outcomes of fights.

Altogether, assessment bias is expected to be a factor influencing weapon evolution and 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 over evolutionary time [47]. Phylogenetic comparative analyses have shown that weapons are highly labile; they can increase in size and complexity, yet equally-so, they readily disappear [25,47,48]. To fully understand weapon diversification, it is essential to consider why weapons, with all their advantages, may become reduced, less robust, or even lost over evolutionary time.

Venom, for example, is a dynamically evolving weapon and the loss of genetic capacity to produce certain component toxins is surprisingly common [e.g., 10,49]. The composition of venom actively coevolves with the physiology of prey and competitors in a coevolutionary arms race. As recipients 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 [50].

Weapons, especially **sexually selected weapons**, can be associated with steep metabolic and survival costs [51,52] and sexually antagonistic effects [53]. 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 can exceed benefits. When they do, selection will reverse weapon elaboration and lead to weapon loss.

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** [54-56]. 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 [54]. For example, electric eels, Genus *Electrophorus,* can generate large electrical discharges – up to 600 volts – without injuring themselves [57]. 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. Similarly, snapping shrimp (Family: Alpheidae) have evolved helmets that protect their brains by dampening acoustic shock waves produced by themselves and others [58].

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.

Animal weapons provide a framework for understanding the evolution of complex, integrated phenotypes

Animal weapons are commonly extreme in their phenotypic elaboration and their physiological demands on the body. Such extremes often result in clear impacts on fitness [3]. Weapons are well positioned for testing general theory across evolutionary biology not only for these reasons, but also because they are directly involved in social interactions, tightly integrated with physiology and behavior, easily measurable, and highly variable within and across populations. In Figure 3 we highlight four areas discussed in this manuscript where weapons may be particularly informative to the field of evolutionary biology as a whole.

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. As such, they hold much potential for providing insects to the field of evolutionary biology as a whole.

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 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 contribute to both the extraordinary diversity of animal weapons and their striking evolutionary lability, including repeated reduction and loss. Ultimately, the diversity we see in animal weapons is not due to any single factor.

Future progress in our understanding of animal weapons, and our ability to gain broad evolutionary insights from these weapons will be enhanced by using 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 the evolution of complex biological systems.

Boxes

Glossary

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

Chemical weapon: Biologically produced chemical substances that can harm other organisms, generally used to facilitate feeding or deter predators or competitors.

Venom: A multi-component chemical weapon often comprised of proteins and peptides that is actively injected to interfere with the homeostatic processes of others Venoms are typically more complex in composition than other chemical weapons.

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: Mitigate the costs associated with the development, use, or maintenance of weapons

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

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

Towards an integrated understanding of animal weapons

Outstanding Questions

To what degree are evolutionary principles shared across different weapon modalities?
Explicit comparisons across mechanical, chemical, electrical, acoustic, and thermal weapons is needed to determine to what degree common rules govern performance, costs, and diversification.

Does phenotypic integration constrain or facilitate responses to environmental change?

Weapons are often ineffective without phenotypic integration among components and supportive traits. When selection acts on one component, does this result in poorly functioning intermediates, slowing the evolutionary response? Or does selection result in coordinated changes in the entire suite of traits?

What are the evolutionary consequences of weapon multifunctionality?
Because many weapons serve multiple roles, future research should examine how competing selective pressures shape trade-offs, constrain optimization, and reduce phenotypic integration within weapon systems.

How are weapon mechanics shaped by ecological contexts and phenotypic plasticity?

Evolutionary biomechanics has often taken a macroevolutionary view. However, the ecological contexts where weapons are grown and used should affect weapon performance and modify evolutionary trajectories.

How do mechanical strength and skill intersect?
Combat outcomes are often understood as the result of mechanical constraints: more muscle, greater force, and therefore a higher likelihood of victory. But skill, learning, and experience may compensate for material disadvantage—a skilled fighter may yet defeat an opponent that is better-armed, but less skilled. The role of skill thus creates an unresolved tension: to what extent can it temper the supposed dominance of mechanical constraints?

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

Declaration of interests

The authors declare no competing interests.

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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* [63]. Snails in the genus *Conus* use a *chemical weapon* delivered via a small harpoon to subdue prey [9]. *Electrical weapons* include the electrical discharge of electric eels, genus *Electrophorus*. This weapon first stimulates prey to move and so reveal itself, and then to freeze, aiding its capture [57]. *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 [58]. 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, numerous 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 [64,65]. While five weapon modalities are featured here, we do not claim this list of modalities is complete. 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 [66] (below). The tapered spiral geometry of the horn and the spongy trabecular bone material within the horn and skull serve to absorb impact [13,67]. 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.

Figure 3. Insights gained from the study of animal weapons can be broadly informative to the field of evolutionary biology. Animal weapons are often under strong selection to drive fitness gains via, for example, competition over access to potential mates, prey capture, and predator defense. (A) Tight phenotypic integration across multiple weapon components and supportive traits is thus expected. For example, weapon components evolve in a correlated manner in the leaf-footed bugs, suggesting certain trait combinations improve function [25]. In some cases, the degree of phenotypic integration may be compromised by (B) multivariate selection due to multifunctionality, a problem not unique to weapons. However, animal weapons can provide examples of innovative evolutionary solutions to competing functions. For example, fiddler crabs (Family: Ocypodidae) use their claws for

signaling, fighting, and defense. (C) Long claws are more visible and better for signaling, but these claws deliver weaker squeezing force at the tips. Some species have evolved both long claw length and a means to deliver greater squeezing force – a catching arch and tubercles mid-way along the length – a design that is successful in both signaling and fighting [27]. Animal weapons that also serve as signals not only are constrained or modified by selection to maintain the ability to cause physical harm, but they are also under intricate selection to convey information. Our diagrammatic adaptation of Shannon's Information Theory (D) [68], illustrates that many steps are involved in signaling systems. Information, such as resource holding potential, is conveyed to a receiver through a transmitter, in this case the antlers of cervids such as elk or red deer. The signal is affected by noise, which may add further distortion. Sensory perception is then subject to interpretation, which may be affected by neurological biases. Consistent differences along this pathway may lead to evolutionary modifications and diversification in the transmitter and associated behaviors. In these examples, we feature large sexually selected mechanical weapons for visual clarity, but these principles apply to weapons across sizes, modalities, and mechanisms of selection. Figure created by Miranta Kouvari, Melisa Morales and Emily Green from Science Graphic Design.

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