

## Opinion

## Why Sexually Selected Weapons Are Not Ornaments

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The elaboration and diversification of sexually selected weapons remain poorly understood. Here, we argue that progress in this topic has been hindered by a strong bias in sexual selection research, and a tendency for weapons to be conflated with ornaments used in mate choice. Here, we outline how male–male competition and female choice are distinct mechanisms of sexual selection, and why weapons and ornaments are fundamentally different types of traits. We call for research on the factors contributing to weapon divergence, the potential for male–male competition to drive speciation, and the specific use of weapons in the context of direct fights versus displays. Given that weapons are first and foremost fighting structures, biomechanical approaches are an especially promising direction for understanding weapon design.

**Bias in the Focus and Terminology of Sexual Selection Studies**

Sexually selected **ornaments** (see **Glossary**) and **weapons** are among the most elaborate and diverse traits in the animal kingdom, and their origin and maintenance remains an active research area among evolutionary biologists and behavioral ecologists [1–9]. **Sexual selection** arises from competition (typically among males) for access to mates, and can take the form of **male–male competition**, **female mate choice**, or both. Although both mechanisms are credited with the evolution of exaggerated sexual traits, most sexual selection studies focus on female mate choice (Figure 1). The unfortunate consequence of this bias is that the terms ‘sexual selection’ and ‘mate choice’ are now often used interchangeably [1,5,7,10], and the term ‘ornament’ often refers generally to all sexually selected traits [11,12].

Several factors probably contribute to this bias in research focus and terminology. Darwin's recognition that male–male competition would favor the evolution of weapons, large body size, and other traits that improve the fighting success of a male was conceptually straightforward, and authors have argued that his understanding of male–male competition was ‘essentially complete’ [1]. By contrast, Darwin's suggestion that females could discriminate among males based on aesthetics was initially considered absurd; thus, early sexual selection studies were dominated by skeptics of female choice [13]. Therefore, mate choice has been more controversial and more popular, because its origin and maintenance is more of an evolutionary puzzle. Additionally, weapons may have been considered analogous to ornaments for so long because of our own visual bias that many weapons (e.g., elk antlers) appear to be ornamental.

We believe that imprecise language and failure to recognize the differences between ornaments and weapons hamper progress in our understanding of sexual selection. Here, we outline how male–male competition and female choice are different mechanisms of sexual selection, and why weapons and ornaments are fundamentally different types of traits. These distinctions are important because the evolution of sexual traits via male–male competition versus female choice

## Trends

The potential for male–male competition to drive the elaboration and diversification of weapon morphologies remains one of the most understudied topics in the field of sexual selection.

Progress in our understanding of weapon evolution has been hampered by a strong bias in sexual selection research, and imprecise terminology that erroneously equates all sexually selected structures with ornaments used in mate choice.

We outline how the processes and outcomes of female choice and male–male competition are distinct, and why weapons and ornaments are fundamentally different types of traits.

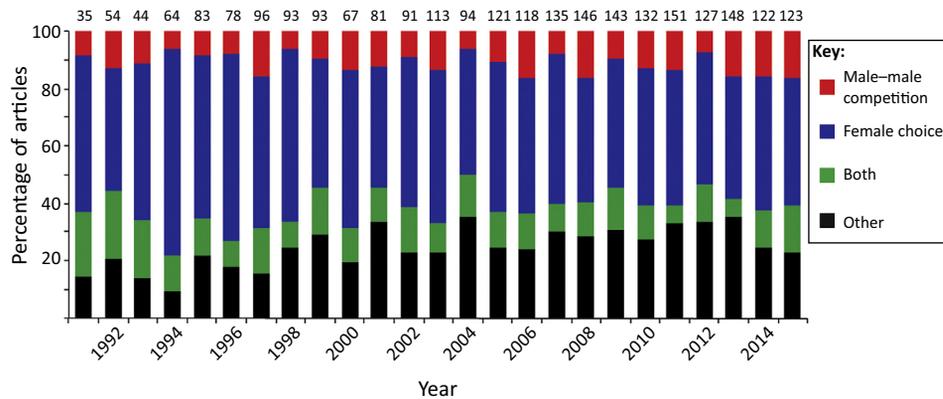
We encourage an integration of engineering techniques into studies of weapon function and performance, and highlight examples of how this biomechanical approach promises to improve our understanding of the evolution of weapon design.

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**Figure 1. Trends in Sexual Selection Research.** There is a bias in the focus of sexual selection research. We examined all sexual selection studies published from 1991 to 2015 in the three main peer-reviewed journals for original scientific research on sexual selection: *Animal Behaviour*, *Behavioral Ecology*, and *Behavioral Ecology and Sociobiology*. Specifically, we used Web of Science to conduct a topic search on the keyword 'sexual selection' for all papers from these journals, and then categorized each study as focusing on: (i) male–male competition; (ii) female choice; (iii) both male–male competition and female choice; or (iv) all other aspects of sexual selection (e.g., female–female competition, male mate choice, or postcopulatory sexual selection). We found that the focus of sexual selection studies has been surprisingly constant over the past 25 years: 50% of studies focused on female choice, while only 12% of studies examined male–male competition. We found an increase in the number of studies that focused on other mechanisms of sexual selection, particularly sperm competition and cryptic female choice, but these studies accounted for only 25% of studies. Thus, studies of male–male competition comprise a mere 12% of the total, despite this mechanism being nearly ubiquitous and clearly an important evolutionary force.

is expected to proceed in different ways, and the study of weapons versus ornaments is likely to require different techniques and approaches.

### Male–Male Competition and Female Choice as Distinct Mechanisms

When Darwin proposed his theory of sexual selection [14], he recognized that the evolution of extravagant male characters could result from one of two mechanisms: male–male competition or female choice. In the case of male–male competition, males engage in direct physical battles with rival males over access to receptive females or resources that attract females (e.g., feeding or nesting sites), and the winners of these contests are more likely to mate with more females. In the case of female choice, males indirectly compete with rivals to attract receptive females, and more attractive males are more often chosen as mates. Of course, the two processes often interact [15,16]: females may incite competition among males and preferentially mate with the winners [17], and males may compete more intensely in the presence of high-quality mates [18,19]. However, the critical distinction between the two mechanisms is that the selective process determining the subset of successful males is mediated by the preferences of the females in the case of female choice, but is independent of those preferences for male–male competition. Understanding the different evolutionary dynamics of ornaments and weapons rests largely on this distinction.

The evolution of female mate choice has been a topic of heated debate since the 1970s, and numerous hypotheses have been proposed to explain the origin, evolution, and maintenance of these preferences, including sensory bias, direct benefits, sexual conflict, good genes, and the Fisher process [5,20]. Given that two distinct traits and their respective loci are involved in the female mate choice process [one expressed in females (the selective mechanism) and one expressed in males (the target of that mechanism)], the evolution of male ornaments should proceed differently from the evolution of male weapons. Specifically, if there is female preference

### Glossary

#### Female mate choice (or female preference):

a form of sexual selection in which females mate nonrandomly with particular males due to a preference for some male trait(s). Female choice favors the evolution of ornaments and courtship displays that make males more conspicuous and/or attractive to females.

#### Male–male competition (or male contest competition):

a form of sexual selection in which males directly compete with rival males for access to females, or resources that attract females. Male–male competition favors the evolution of traits that improve fighting performance, including weapons, large body size, strength, and endurance, as well as aggressive behaviors and signals that effectively threaten and deter rivals.

**Ornament:** for the purposes of this paper, a morphological, acoustic, chemical, or behavioral feature that is expressed by males and is the target of female mate choice.

**Sexual selection:** selection for traits that increase the reproductive success of an individual. Sexual selection is best considered as a subset of natural selection that specifically favors traits associated with competition for access to mates.

**Weapon:** for the purposes of this paper, a morphological feature that is directly used in male–male fights.

for a male ornament, and if there is genetic variation for both the preference and the ornament, then genetic covariance will develop between the two traits [11,21]. Females with the strongest preferences will mate assortatively with males with the most attractive ornaments, and their offspring will carry the alleles influencing the development of both strong preferences and attractive ornaments [5,22]. Therefore, linkage disequilibrium between genes influencing the development of female preferences and male ornaments is expected to arise as an intrinsic consequence of genetic variation in the two traits, and can fuel a positive feedback cycle (the 'Fisher process') that escalates the rate of evolution of ornaments and mating preferences [13,21,23].

By contrast, because there is no female trait that mediates the selection among males in the case of male–male competition, no genetic coupling between male and female traits is predicted to occur [23,24]. Consequently, there should be no equivalent of the Fisher process that escalates the rate of evolution of male weapons. As a result, ornaments have the potential to evolve more rapidly than weapons, although, to our knowledge, this has never been tested. More theoretical and empirical studies on weapon evolution are clearly needed.

Weapons and ornaments also differ in another critical respect: their potential contribution as drivers of speciation. Given the direct link between female preference, mate selection, and reproductive isolation, differences in female mate choice can be a direct barrier to gene flow among diverging populations, and female preference is expected to be a powerful driver of speciation [3,7,21,24–26]. By contrast, there is no direct link between male–male competition and reproductive isolation, and the extent to which male–male competition affects the process of speciation remains poorly understood [27–29].

Although studies have found support both for and against the hypothesis that sexual selection promotes species divergence, a recent meta-analysis found a small but significant positive overall correlation between sexual selection and speciation rate [3]. Intriguingly, the effect of sexual selection on species divergence was generally positive (i.e., supportive) for studies that estimated the importance of sexual selection based on dichromatism, which is likely targeted by female choice, but was negative or ambiguous for studies that estimated sexual selection based on sexual size dimorphism, which probably is favored in the context of male–male competition. To our knowledge, no study has specifically examined whether taxa containing species with elaborate weapons are more or less speciose than those without. Additionally, numerous studies have explored how female preference can contribute to male trait divergence [2,26,30–32], yet surprisingly little is known about how male–male competition can drive the divergence of sexual traits [27–29]. We note that the factors contributing to the variation in weapon morphology, in particular, remain almost entirely unexplored (Box 1).

### Weapons and Ornaments as Similar, but Distinct Traits

To clarify the distinction between ornaments and weapons, we start by highlighting three ways in which they are similar. First, both arise in the context of competition for access to reproduction, a social phenomenon driven by skewed operational sex ratios [33,34], steep Bateman gradients [35–37], or both [38]. This means that the environmental and ecological factors leading to strong selection are likely to be similar for both male–male competition and female choice: when there is a high fitness gain per mating event and when multiple matings can be achieved because individuals of the limiting sex can be readily defended or monopolized, we expect strong selection on both ornaments and weapons.

Second, because the selective environment in both cases is a social one, performance of ornaments and weapons will be relative; what often matters is how well the ornament or weapon of an individual fares in comparison to the ornaments or weapons of other individuals in the

### Box 1. Divergence of Sexually Selected Weapons

The diversity of sexually selected traits has impressed biologists for centuries. Here, we discuss six factors that might have contributed to the diversification of weapon forms (Table I). We anticipate that additional ways by which male–male competition can contribute to trait divergence will be discovered, as weapon evolution becomes a stronger focus of future sexual selection studies.

#### Divergent Fighting Contexts

The most intuitive explanation for weapon diversity is that it reflects selection to maximize performance under different fighting styles. That is, differences in where and/or how species fight can favor corresponding changes in weapon form. This hypothesis can also provide a direct link between weapon divergence and the potential for reproductive isolation: if the weapon type that performs best in combat differs across habitats (e.g., due to the specific nature of fights on different fighting substrates), and if the males possessing well-adapted weapons are more likely to acquire breeding territories, then weapon divergence can enhance reproductive isolation between diverging populations. Specifically, females that prefer to mate in a given habitat will assortatively mate with the males that are the best at fighting within those habitats, thereby suppressing gene flow between populations with distinct weapon types. However, if females do not differ in their choice of breeding habitats, or if offspring are unlikely to end up in the same habitats as their parents, then male–male competition and weapon divergence would have little potential to strengthen assortative mating and the likelihood of speciation.

#### Divergent Costs

Selection to minimize the costs of producing and maintaining weapons can facilitate weapon divergence if weapons differ in the specific costs they incur, and the fitness consequences of these costs vary depending on the habitat and ecology of a species. For example, horn development in dung beetles stunts the growth of neighboring body parts (e.g., antennae, eyes, or wings), and at least part of the diversity in horn types among species appears to have been driven by selection to minimize the relative costs of these resource allocation tradeoffs (e.g., nocturnal species are less likely to have large horns at the base of the head, which would stunt the growth of eyes) [68,69]. That is, individuals with horns that perform well but cost less depending on the particular habitat and ecology of each species appear to have replaced more expensive weapon forms, thereby leading to diversification in the physical location of horns [69].

#### Negative Frequency Dependence

If males bias their aggression towards opponents with similar phenotypes, then rare male morphs can gain a negative frequency-dependent fitness advantage by avoiding costly encounters with most males in the population. Therefore, male–male competition can cause disruptive selection and favor the evolution of divergent male morphologies [27]. There is evidence that such negative frequency-dependent selection has contributed to the variation in nuptial coloration (i.e., visual signals) in African cichlid fishes [28], because males with different color patterns from those present in a given community are more likely to acquire breeding territories than are males with similar coloration. Whether this process can similarly drive the divergence of weapon morphologies is currently unknown.

#### Conspicuous Signaling

As weapons become increasingly important in the context of displays, selection for effective signaling can favor the divergence in weapon shape, color, and/or complexity if the resulting diversity makes the structures easier to assess, but does not reduce their functionality as weapons [26,32]. Conspicuous signaling, at least in the context of dual-function structures that are used both to threaten rival males and attract females [15], could result in assortative mating and, thus, act as a driver of speciation in addition to contributing to weapon divergence. It is less obvious how selection for conspicuous signals that are used in the context of male–male competition alone can drive the speciation process and, to our knowledge, this has yet to be investigated.

#### Fighting Advantage of Novel Forms

Adornments to an existing weapon, such as the addition of tines, tubercles, or spirals, can give the bearer a competitive advantage in combat if opponents lack an effective counterattack or are taken by surprise [24]. Therefore, male–male competition might favor weapon diversification due to the inherent fighting advantage enjoyed by novel weapon forms [70].

#### Chance Events

Game theory models of weapon evolution predict that investment in weaponry can be evolutionarily unstable, such that populations will cyclically fluctuate between periods of high and low investment in weapons [71–73]. The repeated loss

and gain of weapons as predicted by these evolutionary cycles can set the stage for weapon diversification, because chance events in weapon development at the beginning of a new cycle might be enough to start a population along divergent evolutionary trajectories [24,70].

Table 1. Alternative Hypotheses for Weapon Diversification

| Hypothesis                        | Predominant Mechanism Underlying Divergence  | Predictions   | Examples  |
|-----------------------------------|--|---|---|
| Divergent fighting contexts       | Selection to maximize fighting performance combined with changes in fighting context (e.g., fighting substrate) drives changes in weapon form                              | Different weapon types are used in different ways; different weapon types perform better under different fighting conditions                        | Ungulate horns [53,54]; rhinoceros beetle horns [64,74]                       |
| Divergent costs                   | Selection to minimize the costs of producing and/or maintaining weapons favors different weapon forms among species depending on which are the least costly                | Different weapons are costly in different ways; the magnitude of these costs depends on the habitat and ecology of each species                     | Dung beetle horns [68,69]   |
| Negative frequency dependence     | Intense aggression towards similar competitors favors divergent male phenotypes  | Rare male morphs enjoy a fitness advantage by avoiding aggressive encounters with males of the most common morph                                    | No weapon examples yet, but possibly nuptial color variation in cichlids [28] |
| Conspicuous signaling             | Selection for effective signaling (either towards rival males or females) favors different weapon forms depending on which are the most conspicuous in a given environment | Weapons are regularly used as signals, and different weapon forms are more conspicuous in different environments                                    | No weapon examples yet, but possibly color signals in sticklebacks [75]       |
| Fighting advantage of novel forms | Evolution of adornments to an existing weapon (e.g., addition of tines or spirals) gives males a competitive advantage in fights   | Males with novel weapons enjoy a competitive advantage, perhaps in part because opponents lack an effective counterattack                           | None yet  |
| Chance events                     | Evolutionary cycles (i.e., repeated losses and gains) combined with chance events in weapon development generates diversity in weapon form                                 | Weapon diversity is highest in clades that have undergone cyclical arms races and, therefore, have experienced repeated losses and gains of weapons | None yet  |

population at that time [24]. Since this social environment evolves in tandem with the mean value of the trait, selection on both ornaments and weapons will often be more consistently directional than selection acting on other nonsexual traits (e.g., ecological traits, such as beak shape, can approach a performance optimum [24,39]).

Finally, both ornaments and weapons often exhibit strong condition dependence; therefore, exposure to poor nutrition, pathogens, and other forms of stress results in the development of stunted traits, and only the best-conditioned males are capable of producing large and elaborate traits [6,40–42]. As a result, ornaments and weapons are often more variable than other nonsexually selected traits, which makes them especially informative for choosy females and rival males [43,44]. That is, females should benefit from evaluating males on the basis of their ornaments because they can thereby select high-quality males, and males should benefit from assessing the weapons of potential rivals by avoiding the costs of direct, escalated fights with males that are competitively superior. Thus, both ornaments and weapons are frequently used as intraspecific signals of male quality.

Weapons, of course, have an additional role: they are used directly in fights. In fact, weapons are first and foremost fighting structures; even species that primarily use weapons in aggressive displays can inflict real harm on their opponents [15,45,46]. More importantly, even if weapons are selected to become more conspicuous or more effective in displays, they cannot become so elaborate that they are entirely ineffective in fights because they are, at least occasionally, still tested in battle [15,47]. Thus, the fundamental distinction between ornaments and weapons is that ornaments are essentially pure, aesthetic signals, while weapons are typically both signals as well as, and more importantly, functional and mechanical structures (Box 2).

### Box 2. The Weapon–Signal Continuum

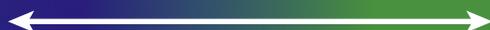
We propose that structures that are favored by male–male competition are best seen as part of a continuum, with pure weapons that are only used in direct combat located at one extreme, and pure signals that are used to threaten rivals and potentially also attract females at the other (Figure 1). Examples of pure weapons may include rhinoceros beetle horns and stag beetle mandibles that are used as tools to lever and lift opponents off resource sites or females during male–male contests [74,76], but are likely to have only a minor role (if any) in visual signaling, given that most species are nocturnal. We note that males may still assess opponents in these systems [77], but chemical, acoustic, or other sensory signals are probably the target of this assessment, rather than visual assessment of the weapon itself. Examples of pure signals may include the eye spans of stalk-eyed flies, which are important in determining the outcome of male–male fights [78], but are not themselves used directly (i.e., mechanically) during fights.

Many weapons, such as claws and antlers, are also used to signal fighting ability [45,55], such that contests are typically resolved by assessment before escalating to costly fights [79]. Of course, claws and antlers can inflict real damage on opponents if a fight ensues [45,46,52], so these structures are best described as having a dual function as both an effective weapon and a signal, and, therefore, belong in the middle of the weapon–signal continuum. The specific location of these traits along the continuum depends on how frequently they are used in the context of direct fights versus displays.

We expect that this continuum framework will shed new insights into the selective pressures acting on weapon morphology. Specifically, we predict that selection on mechanical performance will decrease, and that selection on conspicuousness will increase, as the structure becomes preferentially used in displays, rather than bearing actual loads during fights. Therefore, we predict that weapons will become more complex (e.g., addition of tines or spirals), colorful, and/or will be used in tandem with motor performances (e.g., waving displays) to draw attention to, and enhance the visual appearance of these structures, as they become increasingly valuable as signals. Importantly, we expect that the effect of selection will be similar regardless of whether the signal is used to court females or deter rival males: the most exaggerated and conspicuous traits should be found among species that primarily use them in the context of displays, while the strongest and most robust structures should be found among species that almost exclusively use them directly in fights [80]. Closely related species that differ in how often they use their weapons in the context of fights versus displays should offer the best systems for testing this hypothesis. Therefore, biomechanical studies on weapon morphology may be particularly informative in understanding interspecific patterns of weapon form.



Weapon



Signal

Trends in Ecology &amp; Evolution

**Figure 1.** Structures favored by male–male competition span a continuum from pure weapons that are used in direct physical combat with rival males (left) to pure signals that are used in displays to threaten rival males (right). The precise placement of the examples given here is speculative because the frequency with which weapons are used in the context of fights versus displays is generally unknown and can also differ among closely related species. Selection on mechanical performance of the structures is expected to decrease, and selection on conspicuousness is expected to increase, as the traits become increasingly important for displays. From left to right: stag beetle mandibles (Photo: Juan Carlos Oteyza), elk antlers (Photo: Alison Morris), fiddler crab claws (Photo: Patricia Backwell), and stalk-eyed fly eye spans (Photo: Gerald Wilkinson).

### A Biomechanical Approach to the Study of Sexually Selected Weapons

Given that weapons are essentially 'tools' to pry, pinch, shove, and strike opponents, it only makes sense that a comprehensive understanding of weapon evolution will require an in-depth investigation of the functional aspects and, thus, the mechanical properties of these structures. That is, we simply will not understand weapon diversity unless we understand their underlying biomechanical functions.

Researchers have recently proposed a new 'functional approach' to sexual selection studies that integrates the fields of comparative physiology and functional morphology to gain mechanistic insight into how individuals sustain themselves during energetically demanding contests, and how their musculoskeletal systems allow them to perform the dynamic movements that are required during fights [48,49]. We agree with the advocates of this approach, and argue further that sexual selection researchers should seek collaborations to gain insights into the mechanical design of the weapons themselves. We suggest several avenues for future research that promise to expand our understanding of weapon design.

First and foremost, we need more information on how weapons are used in fights. Ungulates are by far the most well-studied taxa in this regard; comparative analyses have found correlations between weapon morphology and species-specific fighting styles, suggesting that differences in how or where males fight favor corresponding changes in weapon form [50–54]. For example, bovid species with short, smooth horns tend to be stabbers; species with robust, curved horns tend to be rammers; and species with long, reaching horns tend to wrestle and fence [51,53]. Whether these patterns are found in other taxa is still largely unknown.

Careful observation of fighting behaviors is also important for understanding the mechanics of weapons and, thus, the specific forces that males can generate and impose on opponents during fights. For example, male fiddler crabs have an enlarged claw that is used both as a visual signal to attract females and threaten males, and as a weapon in fights [55,56]. Longer claws are more effective signals, but are also less effective weapons because the mechanical advantage and, thus, the amount of force a male can transmit, decreases with claw size [57]. However, recent observations have shown that males grip opponents at tubercles on the inner margins of the claw fingers, rather than at the tip, which allows large claws to be both effective signals and powerful weapons [47]. Therefore, close examination of the fighting style of an animal is essential for making accurate predictions about the magnitude of forces males can deliver on opponents, and how well their weapons will perform in fights [58].

Second, variation in material properties, independent of geometry, can affect how structures perform [59], so we need detailed information about the materials from which weapons are made. For example, antler bone is one of the toughest, most fracture-resistant biological materials known, which allows antlers to withstand the high-impact, head-on collisions that occur during fights [60]. Material properties can also place a mechanical limit on maximum weapon size [61] or how the weapons can be used in contests. Thus, studies that compare material properties across species can offer important insights into differences in weapon size and how fighting behavior coevolves with weapon design. Whether the material properties of weapons are tuned to species-specific fighting styles remains to be tested (but see [62]).

Finally, biomechanical modeling promises to be a particularly useful tool for answering long-standing questions about weapon diversity. In particular, the application of mature engineering techniques, such as finite element (FE) analysis [63], will allow researchers to rigorously test the form and function of weapons in a way that is not possible with animals in the field. For example, using FE analysis, researchers can subject a weapon to forces that it both does and does not experience under normal fighting conditions to explicitly test whether different weapons are

structurally adapted for specific fighting styles [64,65]. The ability to digitally manipulate the morphology of these models [66,67] also makes it possible to evaluate the functional significance (if any) of specific features (e.g., tubercles, forks, and grooves) that distinguish the weapons of different species.

A recent study on rhinoceros beetle horns demonstrates the utility of the biomechanical modeling approach: McCullough *et al.* [64] constructed FE models of the horns of different species, and compared their performance under both species-typical and species-atypical fighting loads. The horns were found to be both stronger and stiffer in response to species-typical fighting loads, and to perform more poorly under fighting loads characteristic of other species. Additionally, the performance differences could be attributed, at least in part, to variation in cross-sectional horn shape [64]. These results suggest that horns are structurally adapted to meet the functional demands of fighting, and that selection for improved performance under different fighting styles has had an important role in the diversification of horn morphology. We believe that the integration between biomechanics, evolution, and behavior is critical to a full understanding of the diversity of weapon forms and, therefore, is an exciting and promising new direction for the field of sexual selection.

### Concluding Remarks

Our understanding of the evolution of weapons via male–male competition is far from complete. For example, we still know surprisingly little about the patterns of weapon diversity among closely related species, the potential for male–male competition to drive trait divergence, or whether male–male competition acts as an engine for speciation. We encourage further empirical, theoretical, and comparative studies on the evolution of weapons to address each of these questions, and expect that a biomechanical and functional approach will be particularly informative for explaining the details of weapon design. Although female choice has been more controversial and, thus, more popular for evolutionary biologists, it is important that sexual selection does not inadvertently become synonymous with female choice, because female choice is just one component of sexual selection. Similarly, while many weapons might appear ornamental, it is important that our own visual bias does not obscure the important differences between the two classes of sexually selected traits. Indeed, our understanding of the full range of extravagant male characters will be incomplete unless we address how these structures are used in the context of both fights and displays (see Outstanding Questions).

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### Outstanding Questions

What are the evolutionary drivers of weapon diversification? If male–male competition is not directly linked with barriers to gene flow, can this process drive speciation [27–29]? Does weapon divergence drive reproductive isolation, or vice versa? Are taxa containing species with elaborate weapons more speciose than those without?

What are the evolutionary drivers of weapon exaggeration? Why do sexually selected weapons reach extreme proportions in some species, but remain unexaggerated in others? What conditions favor the evolution of extreme weapon size?

How does weapon morphology coevolve with fighting behavior? Does selection act first on fighting behavior and then on weapon design? Or do weapons diversify first and then fighting behaviors are selected to make the best use of the existing weapon forms?

Is escalated evolution of sexually selected weapons a coevolutionary process (i.e., an arms race)? If so, then what are the relevant traits and/or loci (e.g., habitat preferences and weapon form, fighting styles and weapon form, offensive and defensive tactics)?

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