

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.

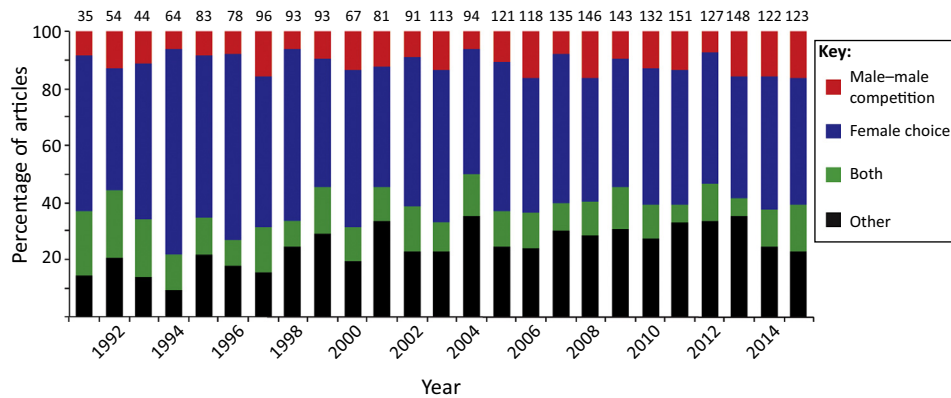
We encourage an integration of engineering techniques into studies of weapon function and performance, and highlight examples of how this biomechanical approach promises to improve our understanding of the evolution of weapon design.

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Trends in Ecology & Evolution

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.

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