

Commentary on Invited Review

By any name, female–female competition yields differential mating success

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In this review, I use the body of literature on female–female aggression as a platform to identify how females compete for mates. I also examine the ways in which this competition is similar to and different from the male counterpart, a key step in the development of a unified theory of sexual selection that incorporates the variety of ways in which members of the same sex compete for mates. Responses to my review indicate both a deep interest in female competitive interactions as well as a difference of opinion on how to approach this topic, reflecting a consensus on the importance of the subject, amid conflict on technique and word choice. Most importantly, these commentaries collectively underscore the need for greater attention to functional variation in female phenotype and the development of an evolutionary theoretical framework for female competitive interactions.

The research that I highlight suggests that female–female competition that yields variance in female mating success is quite widespread. I fully support the commentaries in advocating rigorous experimentation, so that we can place these phenomena within evolutionary and behavioral ecological theory, alongside male–male competition for mates, as an important driver of phenotypic evolution. There are many additional ways in which female phenotypic variation affects fitness outside the realm of competition for mates (summarized nicely by Gowaty 2011), and these too should be investigated. There will be empirical difficulties, many of which are articulated by both While and Robinson (2011). Several commentaries echo the need to establish how selection shapes phenotypes in both sexes, without assumptions about the nature of sex differences. These tests should include selection differentials, trade-offs, and the ecological determinants of phenotype in both sexes (Robinson 2011). In particular, Robinson's call for greater integration of genotype-by-environment interactions into the study of sexual selection and sex differences points to a potential source of novel findings. Future work should also test how the sexes balance competitiveness and choosiness, and whether males and females use the same rules of engagement throughout the myriad ways in which they compete for mates (Forsgren 2011). At each of these turns, we need to test when and why the outcome of same-sex competition yields similar fitness benefits in the 2 sexes and when and why it does not.

Some of the commentaries raise concerns surrounding semantics and the definition of sexual selection that I use, whereas others agree that “competition for mates” is an appropriately broad characterization, after Shuker (2010). Ah-King (2011), Gowaty (2011), and Robinson (2011) argue that semantic discussions distract from the ultimate goal of understanding the evolution of competitive phenotypes in females. I agree that the focus should be the process—that females vary in one or another trait, and this variance predicts the outcome of female–female competition and ultimately mating success. However, semantics are not irrelevant. Even though common parlance disregards semantics as trivial (“just semantics”), se-

manantics are the study of meaning, and semantic discussions are helpful in resolving problems of understanding related to word choice (e.g. with epigenetics, see Crews 2008). Alternatives to my approach include avoiding the term sexual selection, focusing only on process, and/or using entirely different words (Clutton-Brock 2009, Gowaty 2011; West-Eberhard 1983). Given the clear parallels between sexual selection in males and many of the patterns in my review, these options seem unlikely to satisfy. In addition, the term sexual selection comes along with a broad (albeit imperfect) theoretical framework with clear testable hypotheses, some of which are remarkably unexplored in half of the population (i.e., in females). Furthermore, confusion over terms can have grave implications if gender biases steer us away from patterns in nature (Gowaty 1997; Karlsson Green and Madjidian, 2011, and commentaries, this volume). If we continue to avoid the term sexual selection when studying female–female competition for mates, but use the term at will in males, will the female perspective continue to be relegated to a less evolutionarily significant position relative to the male equivalent? If we instead appreciate and test the ways in which females compete for mates and the ways in which this competition is both similar to and different from male–male competition, perhaps, the synthesis of these 2 approaches will lead us toward greater advances (Kuhn 1962).

Disagreements over sexual selection have persisted for nearly as long as the term has existed. Gowaty and Ah-King subscribe to one side of this debate when they criticize my characterization of sexual selection. I disagree that sexual selection was clearly defined by Darwin only in the broad way they describe, where it is synonymous with nearly all selection on reproduction. This broad conceptualization neglects Darwin's own clarifications that sexual selection is more narrow than any same-sex competition related to reproduction. Rather, it occurs when some individuals do not obtain a mate, obtain “retarded or less vigorous” mates or obtain fewer mates than others (Darwin 1871, p. 226). This statement lies at the heart of my assertion that competition for mates can occur in many ways, some more subtle than others. To equate sexual selection with other forms of natural selection is to minimize the fascinating evolutionary dynamics that often occur between the 2. Sexual selection was put forth to explain the bizarre (though retrospectively intuitive) observation that phenotypes with no advantage in health, offspring nourishment, survival, etc. can still be favored simply because they influence competition for mates. This review does not aim to resolve the debate over the definition of sexual selection, nor does it aim to distinguish between natural and sexual selection in every possible example, a likely futile goal (Darwin 1871 p. 210). Instead, I contrast the 2 to provide a conceptual milieu in which to place the numerous and clear examples where intrasexual aggression among females yields differential mating success.

Ah-King's critique of Bateman highlights some excellent points regarding the imperfect framework surrounding sexual selection. Researchers often assume sex differences in Bateman gradients (i.e., positive covariation between reproductive success and the number of mates in males but not in females), but there are many species in which mate number positively covaries with female reproductive success (e.g., Evans and Magurran 2000; McLeod and Marshall 2009; Schulte-Hostedde et al. 2004; Tregenza and Wedell 1998; Wiebe and Kempnaers 2009).

Notably, few of these studies have examined the causal factors that result in variation in female mating success or reproductive skew. In the near future, I hope we will better illuminate the causal links between competitive ability, mating success, and reproductive success in females. A study by While and colleagues (2009) demonstrating positive relationships between female aggressiveness and the number of extrapair offspring provides correlational support for the hypothesis that competitive phenotypes predict mating success, but experimental tests are warranted before causally linking the 2.

The predictions that I lay out and the conclusions I draw in my review are based on the limited pool of data regarding competitive interactions among females, and as such, they are not intended to be the final word on the subject but rather to serve as a starting point. The scope of questions and approaches suggested by my review and the commentaries provide a multi-pronged way forward, with my synthesis of the past providing testable predictions and priorities for the future. Clearly, there is much exciting work yet to be done.

Key words: female aggression, female competition, sexual selection.

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