

Editorial

Male mate choice, female competition, and female ornaments as components of sexual selection

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Choosing a mate is likely one of the most influential decisions any individual makes because it heavily influences their fitness. Going back all the way to the seminal work by Darwin (1871, 1859), we mostly think of females as choosing mates, whereas males compete over mating opportunities with females. This view is very well supported, but somewhat incomplete. As Darwin struggled to find a good explanation for the existence of ornamental traits in males, he proposed Sexual Selection and along with that theory he suggested 2 mechanisms that could lead to and maintain such extreme traits: Female Choice and Male Competition. Historically, male competition was quickly accepted, whereas acceptance of female choice was delayed until much later, coinciding with the rise of modern feminism (Zuk 1993).

Later, germane work by Bateman (1948), Trivers (1972), and Lehtonen et al. (2016) established that the early investment into gametes is extremely important in defining what is known as “sex roles.” In a nutshell, males invest very little into individual gametes as compared to females, which make very strong investments into their eggs. This concept of ‘sex roles’ has created a somewhat binary view of a phenomenon that is actually quite continuous (Ah-King and Ahnesjö 2013). Consider investments into offspring made by males after fertilization of the eggs. In some cases this has led to the evolution of “sex role” reversal, where the males act choosy, and females compete over males (Berglund and Rosenqvist 2003). In less pronounced cases, however, males may also invest into their offspring, which may lead to the evolution of choosiness in males. But this is not the only scenario for the evolution of male mate choice, and one relatively often reported phenomenon is the presence of male mate choice when females differ strongly in quality (Edward and Chapman 2011). In this case male mate choice might even evolve when males contribute nothing but sperm to their offspring.

The theoretical literature on male mate choice is by far not as well developed as the one on female choice. One aspect that I find particularly important is that—in contrast to the evolutionary impact of female choice on males—it is unlikely that traits in females evolve to be detrimental to females, as many ornaments are in males (Fitzpatrick and Servedio 2017, 2018). This seems to be because

male fitness directly depends on female fitness, and most reductions of female fitness are also costly to males. The limited existing literature is reviewed and summarized by Fitzpatrick and Servedio (2018). One of the important conclusions is that genetic constraints, mainly via pleiotropy can be powerful. Another key conclusion from their work is that we know too little about the effects of male mate choice on the evolution of female ornaments. This article will provide excellent guidance for future studies, both empirical and theoretical. Clearly, male mate choice is not simply the inverse of female choice.

Conceptually, male mate choice is not only connected to female mate choice, but also relevant to our understanding of female–female competition, and female ornamentation. Although ornamentation in females may be due to pleiotropy, it can also evolve in response to male mate preferences. Two studies in the Special Column discuss such scenarios. One study by Weiss and Dubin (2018) investigates how male *Sceloporus* lizards adjust reproductive effort based on ornament size in females. The effects are subtle, but males do base their decision to engage in male–male competition on the perceived reproductive benefit provided by females. The other study is by Yong et al. (2018) and investigates the relationship of female ornamentation and female aggression in two populations of sticklebacks. Interestingly, the expression of the ornament (red coloration) does not correlate directly with female aggression. Both studies are important as they raise relevant new questions.

Another female trait that might be influenced by male mate choice is female competition. Of all the aspects connected with male mate choice, this might be hardest to grasp. Just like male mate choice is not simply the inverse of female mate choice, female competition appears to be more indirect, at least apparently, and typically lacks the open fights that characterize male–male competition. The same principle might be behind this: if female viability is imperiled, such traits may be difficult to evolve. By contrast, females compete with each other for many resources, including males, but such interactions may be difficult to measure and hard to observe (Heubel and Plath 2008). In a paper on a small fish, the common goby, Heubel (2018) elucidates how females respond to female

competition for large, nest holding males. Her work especially highlights the role of the operational sex ratio as a crucial factor in mate choice and female competition.

Another paper—also on gobies—by Amundsen (2018) reports a similar effect. The operational sex ratio in another small fish, the two-spotted goby, is key to a functional sex role reversal over the breeding season. This mating system is characterized by an overabundance of males early in the season. Late in the season, however, females become more abundant and compete for males (Borg et al. 2006). This is remarkable because it provides an insight into a temporal dynamic that might be much more widespread, but difficult to observe. This mating system may provide an especially elegant explanation for the presence of ornaments in both sexes.

Finally, in my own paper (Schlupp 2018), I review male mate choice in a group of fishes that shows no male parental investment, livebearing fishes (Poeciliidae). Somewhat surprisingly male mate choice is widespread in that taxonomic group, and seems to be mostly associated with differences in female quality. Overall, males seem to prefer larger, more fecund females. One point I am trying to make in this context is that apparently similar preferences can be present in females and males, but their evolutionary origin may be different. Consider the widespread preference for larger size found in both males and females. In the case of female choice this preference is often interpreted in the context of indirect benefits, in particular in polygamous species. By contrast, male preferences for larger females are typically viewed as a direct benefit to males via higher fecundity found in larger females. I think this makes comparative studies of female and male preferences especially interesting. I feel that more studies looking at mate choice in both sexes of a species using the same experimental method would be great (Ptacek & Travis 1997; Justus and Mendelson 2018).

The present Special Column provides glimpses of the phenomena associated with male mate choice and hopefully creates a more holistic view of mate choice and sexual selection in general. Due to my own research interests and limitations, the articles compiled here are taxonomically very biased toward vertebrates, but there is exciting work done on many other taxa. The literature on insects, for example, is nicely summarized by Bonduriansky (2001). Maybe, we are able to stimulate future research, both theoretical and empirical, into the topics presented here. I think the most important aspect to understand more fully is how male and female mate choice as well as male and female competition interact to produce the outcomes we observe in nature, especially mutual mate choice.

Acknowledgments

Many of the contributors of this special column met in the summer of 2017 for a symposium in Estoril, Portugal. The title of the symposium was “Integrating Male Mate Choice, Female Competition, and Female Ornaments” and the participants and discussants lived up to the expectations:

the discussions were lively, engaged, and open. I am very grateful to all of them. I also am deeply grateful to the organizers of the *Behaviour* conference, who hosted the symposium. They created a warm and friendly atmosphere that allowed for the delightful and productive interactions we had.

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