

## **eLetter response to “Darwinian sex roles confirmed across the animal kingdom” by Janicke et al. Research article, February 2016, in Science Advances**

Janicke et al. [1] conduct a meta-analysis of Bateman metrics, and conclude that their analysis confirms Darwinian “sex roles” across the animal kingdom [1]. They show that both the opportunity for selection and the Bateman gradient are more often greater in males, whereas the opportunity for sexual selection was slightly, but not significantly, higher in males than females. Overall the average for all three estimates was biased towards males, but the data also include studies with unbiased or female-biased estimates. This is an important and impressive analysis, but we do not agree that it supports the main conclusion the authors have drawn from it. On the contrary, while we are optimistic that further studies like this one will clarify much about how sexual selection promotes diversity, we worry that the unidimensional “sex role” view advocated in this paper will not be helpful to scientific progress. In order to advance science, we need to acknowledge and understand the diversity and patterns in sex-biased sexual selection, as well as its ecological influences. We will explain how distilling this variation to a single “sex role” does little to test Darwin’s and Bateman’s ideas.

### **Darwin’s principle of sexual selection can cause diverse patterns**

First, we would like to contest the implicit premise that there should be a universal “sex role” based on the principles of sexual selection, and that “exceptions” somehow undermine evidence for sexual selection. This logic concedes too much to recent (and in our view, confused) arguments against the importance of sexual selection for explaining diversity in sexual behavior. If Janicke et al. [1] had not found an overall trend towards stronger sexual selection on males, that would provide as little justification for ditching sexual selection theory as their current findings provide for a universal “sex role”. The diversity in mating behavior is best explained by appealing to sexual selection, which can comfortably account for populations and species in which sexual selection is not stronger on males. The occurrence of a common pattern in nature is interesting, but it is neither Darwinian, nor advancing science to make this pattern a universal rule across animals. Our aim should instead be an evolutionary understanding of how selection explains variation around the mean as well as the mean itself.

### **Problems with the “sex role” concept**

The authors’ conclusions are partly undermined by problems associated with the “sex role” concept, which fails to acknowledge important and fascinating multidimensional variation in sexual behavior that is not well quantified by the authors’ metrics. Janicke et al. [1] argue that most animal mating systems should exhibit a conventional Darwinian “sex role”, characterized by “female-biased parental care and male-biased sexual dimorphism”. But these two characteristics are not opposite poles along a single dimension of variation: strong sexual

selection on one sex need not prescribe weak selection on the other. For example, mating systems featuring strong sexual selection on females are fascinating in part because female polyandry often enhances the intensity of postcopulatory sexual selection on males. Any good comparative analysis of diversity ought to distinguish rather than combine measures of the intensity of parental care, sexual dimorphism, and sexual selection.

It is worth noting that Darwin [2] neither used the phrase “sex role” nor the term “conventional”. Instead, he argued that (pre-ejaculatory) sexual selection leads to the evolution of secondary sexual characters. He wrote that sexual selection “depends on the advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction”, and did not confine this principle to a particular sex. Darwin provided many examples of sexually selected traits in males, but he also gave examples of secondary sexual characters in females. The packaging of various traits and abilities into a single “sex role” has a long history of being questioned. For instance, Gwynne [3] argued for the separation of “sex roles” into courtship roles and parental roles. Vincent et al. [4] clarified, as a convenient shorthand, the “reversed” sex role in which “females compete more intensely than males for access to mates” (in contrast to a conventional role where males compete more intensely for access to females). However, a review of the “sex-role” concept [5] revealed a lack of consensus around its usage and what to include (or exclude) in assessing it. The three main problems with the “sex-role” concept are: i) that its use is typological and stereotypical, ii) it separates a continuous range of variation into two discrete categories and iii) it masks variation found within and among populations. Janicke et al. [1] define a conventional “sex role” as female biased parental care and male-biased sexual dimorphism, but this package is problematic when applied over the animal kingdom because parental care is actually relatively infrequent. For example, many insects and fishes lack parental care, and in fish, when parental care occurs it is more commonly male-biased, and often associated with male-biased sexual dimorphism.

### **Understanding the diversity in sexual selection across animals**

Janicke et al. [1] depict a “sex role” syndrome in their Fig. 3 and state that “sexual selection is stronger in males than in females, which must, by definition be rooted in anisogamy”. Anisogamy defines males and females, but it does not define in which sex sexual selection is stronger. Sexual selection is more commonly stronger in males, as demonstrated in this meta-analysis, but if this was so by definition we would not see the diversity presented in Figure 1. Furthermore, as acknowledged by Janicke et al. [1], causality can work both ways i.e. parental investment may govern sexual selection [6] and sexual selection may translate into parental investment [7]. This latter scenario means that when sexual selection is sex-biased, the future reproductive prospects can influence the parental care pattern as much or more than past investments (like gamete size) [8]. Sexual selection is influenced by many more factors than gamete size alone, as already argued by Trivers [6] when presenting his parental investment ideas, phrased without sex specific confinements.

## To advance science

Advancing our understanding of sexual selection will undoubtedly be facilitated by meta-analyses of metrics like those compiled by Janicke et al. [1], not least because these analyses demonstrate diversity in as well as overall averages for sexual selection. We are, however, dismayed by the conclusion confirming the generality of a so-called Darwinian “sex role” across the animal tree. This view is surprisingly constrained, and belittles critical earlier work (as worthy of the Darwinian tradition as any other research) that has clarified how sexual selection has resulted in diversity among animals.

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## References

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