

Is sexual selection defined by dimorphism alone? A reply to Padian and Horner

Robert J. Knell¹, Darren Naish², Joseph L. Tomkins³, and David W.E. Hone¹

¹ School of Biological and Chemical Sciences, Queen Mary University of London, Mile End Road, London, E1 4NS, UK

² Ocean and Earth Science, National Oceanography Centre, Southampton, University of Southampton, Southampton, SO14 3ZH, UK

³ Centre for Evolutionary Biology, The School of Animal Biology, The University of Western Australia, WA 6009, Australia

In their letter in response to our article in *TREE* [1], Padian and Horner [2] make three main points, the two most relevant concerning firstly the definition of sexual selection itself and secondly, the issue of how we might test for its presence in fossils organisms. Their third point pertains to species recognition and is addressed by Mendelson and Shaw [3].

Padian and Horner [2] employ what we think is a restrictive definition of sexual selection which requires sexual dimorphism to be present. They claim that ‘Because Darwin invented sexual selection, and based it on observations that have never been falsified, his definition cannot be wrong.’ It may be true that Darwin’s definition cannot be considered ‘wrong’ without falsification, but this does not mean that scientists cannot or should not modify or use alternate definitions based on evidence that has accumulated since Darwin’s time. Scientific definitions are subject to change because we alter theories and definitions to account for evidence, or use multiple definitions depending on context.

Thus researchers should not be dogmatic about definitions of sexual selection, regardless of who created that definition or their intent at the time. Furthermore, we think the basis of Padian and Horner’s argument is questionable: although the observation of sexual dimorphism spawned Darwin’s idea, in neither *The Origin of Species* nor *The Descent of Man* can we find an unambiguous definition of sexual selection requiring sexual dimorphism. In fact, we find quotations in Darwin’s work that instead demonstrate an openness to the possibility of sexual selection operating in the absence of sexual dimorphism:

‘There are, however, many animals in which the sexes resemble each other, both being furnished with the same ornaments, which analogy would lead us to attribute to the agency of sexual selection. In such cases it may be suggested with more plausibility, that there has been a double or mutual process of sexual selection; the more vigorous and precocious females selecting the more attractive and vigorous males, the latter rejecting all except the more attractive females’ ([4] p. 225). Although Darwin goes on at this point to reject sexual selection as an explanation in this instance (for what we would now term ‘genetic correlation’), it is not because of a lack of dimorphism.

Padian and Horner’s definition of sexual selection [2] requires sexual dimorphism to be present and excludes mutual sexual selection, the phenomenon whereby members of both sexes bear exaggerated structures [5], and so also contradicts Darwin’s own comments. Padian and Horner’s definition is also restricted to structures or behaviours that ‘attract mates or repel rivals for mates’ [2] and therefore also excludes postcopulatory sexual selection and the myriad traits that have evolved because of processes such as sperm competition [6]. For these reasons we favour hypotheses about sexual selection drawn from an understanding of the process; Darwin articulated how sexual selection differed from natural selection by stating that sexual selection occurred where the selection ‘depends on the advantage which certain individuals have over others of the same sex and species solely in respect of reproduction’ ([4] p.209). This description of the process encompasses intersexual selection and intrasexual competition in all of its forms, including mutual sexual selection, sperm competition, and sexual conflict, and can be present with or without sexual dimorphism. To us, and we think the community of scientists working in this field (e.g., [7]), this definition distinguishes the two forms of selection in the most logical way. Without it, we are at a loss as to how processes such as sperm competition and mutual sexual selection should be discussed, as they are clearly not mediated by conventional natural selection.

With respect to hypothesis testing, Padian and Horner [2] are correct that we do not deal with some of the proposals they put forward to distinguish between species recognition and sexual selection when attempting to explain the presence of exaggerated traits. This is because these proposals had already been addressed in a previous publication [8]. Although we agree with Padian and Horner [2] that rigorous testing of hypotheses is desirable, we hope that our review [1] makes it clear that cases of putative sexually selected traits in the palaeontological record are exceedingly variable in terms of the form of the trait(s) and the nature and quality of the evidence available. This means that careful and flexible thought about testable hypotheses that can distinguish between explanations is necessary [1,9], rather than a demand for specific analyses on large data sets, an approach which we believe will not be helpful in determining trait function in many cases. Sexual selection is so common and so potent an evolutionary force, and is responsible for so much diversity in extant organisms, that to discount it as a similarly powerful force acting

on extinct organisms because of a lack of testing, rather than having failed testing, risks an incorrect interpretation of the fossil record.

References

- 1 Knell, R.J. *et al.* (2013) Sexual selection in prehistoric animals: detection and implications. *Trends Ecol. Evol.* 28, 38–47
- 2 Padian, K. and Horner, J.R. (2013) Misconceptions of sexual selection and species recognition. *Trends Ecol. Evol.* 28, <http://dx.doi.org/10.1016/j.tree.2013.01.011>
- 3 Mendelson, T.C. and Shaw, K.L. (2013) Further misconceptions about species recognition: a reply to Padian and Horner. *Trends Ecol. Evol.* 28, <http://dx.doi.org/10.1016/j.tree.2013.02.012>
- 4 Darwin, C. (1871) *The Descent of Man and Selection in Relation to Sex*, John Murray
- 5 Huxley, J.S. (1914) The courtship habits of the great crested grebe *Podiceps cristatus*; with an addition to the theory of sexual selection. *Proc. Zool. Soc. Lond.* 35, 491–562
- 6 Simmons, L. (2001) *Sperm Competition and its Evolutionary Consequences in the Insects*, Princeton University Press
- 7 Clutton-Brock, T. (2007) Sexual selection in males and females. *Science* 318, 1882–1885
- 8 Knell, R.J. and Sampson, S. (2011) Bizarre structures in dinosaurs: species recognition or sexual selection? A response to Padian and Horner. *J. Zool.* 283, 18–22
- 9 Hone, D.W.E. *et al.* (2012) Does mutual sexual selection explain the evolution of head crests in pterosaurs and dinosaurs? *Lethaia* 45, 139–156

0169-5347/\$ – see front matter © 2013 Elsevier Ltd. All rights reserved.
<http://dx.doi.org/10.1016/j.tree.2013.02.007> Trends in Ecology & Evolution xx (2013) 1–2