Behavioral Ecology Advance Access published March 10, 2016

Behavioral Ecology

The official journal of the ISBE International Society for Behavioral Ecology

Behavioral Ecology (2016), 00(00), 1–2.

Invited Commentary

A response to comments on stress and sexual signaling: a systematic review and meta-analysis

Fhionna R. Moore,[a] David M. Shuker,[b] and Liam Dougherty[c]

[a]School of Psychology, University of Dundee, Nethergate, Dundee DD1 4HN, UK, [b]School of Biology, Biomedical Sciences Research Complex, University of St Andrews, St Andrews, Fife KY16 9TH, UK, and [c]School of Animal Biology, University of Western Australia, 35 Stirling HIghway, Crawley, Perth, Western Australia 6009, Australia

The commentaries on our review (Moore et al. 2015) support our conclusion that understanding role(s) of stress in sexual selection requires modeling of nuanced effects of species ecology, trait ontology, and the complexities of the stress response (e.g., Møller and Saino 2015). They further confirm the need for future research to 1) model roles of stress in interaction with androgens and the immune response (Buchanan et al. 2015), 2) include experimental work to elucidate how stress influences sexual signals and, indeed, whether females can detect these differences (Buchanan et al. 2015; Leary 2015), and 3) consider the roles of stress during secondary sexual trait development (Buchanan et al. 2015; Leary 2015). We predict that continued data collection that takes these points into consideration will address Garamszegi's (2015) valid point that current sample sizes (especially given the nonindependence of many of the results included in our analyses) may be insufficient to detect biologically meaningful associations.

We consider Leary's (2015) suggestion to investigate effects of stress on central structures, such as motor activity, to represent an important future direction that will undoubtedly explain some of the inconsistencies in findings to date, as may his suggestion that we should assess an integrated measure of secondary sexual trait expression as a whole, rather than single aspects of phenotype. We also agree that stabilizing selection, which may act against directional selection for secondary sexual traits, may further obscure any straightforward linear relationship between stress and trait expression. This further supports the need for future work to take into account species and population ecology.

In response to Møller and Saino's (2015) criticisms of our methodology, we argue that although it is true that the methods we used in our meta-analysis are grounded in older approaches, we have used the most contemporary methodology generated by a rapidly developing field (e.g., Hadfield and Nakagawa 2010; Lim et al. 2014; Nakagawa and Santos 2012). We would also counter their suggestion that heterogeneity in measures of baseline glucocorticoids (GCs) may contribute to lack of effects of stress, by pointing out that measures of baseline GCs were taken within 3–5 min of sampling (i.e., prior to the release of GCs in response to the stressor of capture and handling), thus reducing potential heterogeneity. None of the studies we included reported the length of time between capture and blood sampling for individuals, so we were unable to include this covariate in our analyses. We do, however, concur that GCs deposited in feathers, hair, and feces, levels of heat shock proteins, and the heterophil:lymphocyte ratio (which we grouped together as measures of "long-term stress") are likely to provide measures of stress over differing temporal durations, and may therefore have made it more difficult for us to detect effects of chronic stress on secondary sexual trait expression. However, as there were insufficient numbers of studies that used each of these measures, we were unable to test for differences between them. Furthermore, taken in the context of stress measures overall, we felt these 3 measured something significantly different to the other measures included in our analyses (i.e., maximum GCs produced under stress, experimentally elevated GCs, and baseline GCs), but insufficiently different from one another so that, for the purposes of our analyses, we grouped them under the umbrella of "long-term stress."

Finally, we agree with Buchanan et al. (2015) that it is essential to operationalize stress carefully, and for measures of physiological response to stressors to distinguish between adaptive responses to environmental demands, and maladaptive chronic activation of the stress response. In our discussion we argued the importance of distinguishing between, for example, response to unpredictable stressors and predictable seasonal challenges such as the molt; of taking multiple measures of the stress response and long-term stress, and measuring stress history; and of capitalizing on advances in measurement of the stress response, including duration, total GCs released in response to an ecologically valid, standardized stressor, the efficiency of negative feedback, as well as the concentration and distribution of GC receptors.

Address correspondence to F.R. Moore. E-mail: fmoore@dundee.ac.uk.

Received 6 February 2016; revised 23 February 2016; accepted 24 February 2016.

doi:10.1093/beheco/arw034

Editor-in-Chief: Leigh Simmons

REFERENCES

Buchanan KL, Mariette MM, Crino OL. 2015. Stress and sexual traits: why are there no clear relationships? Behav Ecol. 27:374.

Garamszegi LZ. 2015. When limited availability of data meets with a thorough meta-analysis: a comment on Moore et al. Behav Ecol. 27:375.

Hadfield JD, Nakagawa S. 2010. General quantitative genetic methods for comparative biology: phylogenies, taxonomies and multi-trait models for continuous and categorical characters. J Evol Biol. 23:494–508.

Leary CJ. 2015. Is stress sexy? A comment on Moore *et al.* Behav Ecol. 27:373–374.

Lim JN, Senior AM, Nakagawa S. 2014. Heterogeneity in individual quality and reproductive trade-offs within species. Evolution. 68:2306–2318.
Møller AP, Saino N. 2015. Sex and stress: a comment on Moore et al. Behav Ecol. Advance Access published November 27, 2015, doi: 10.1093/arv208.
Moore FR, Shuker DM, Dougherty L. 2015. Stress and sexual signaling: a systematic review and meta-analysis. Behav Ecol. 27:363–371.
Nakagawa S, Santos ESA. 2012. Methodological issues and advances in biological meta-analysis. Evol Ecol. 26:1253–1274.