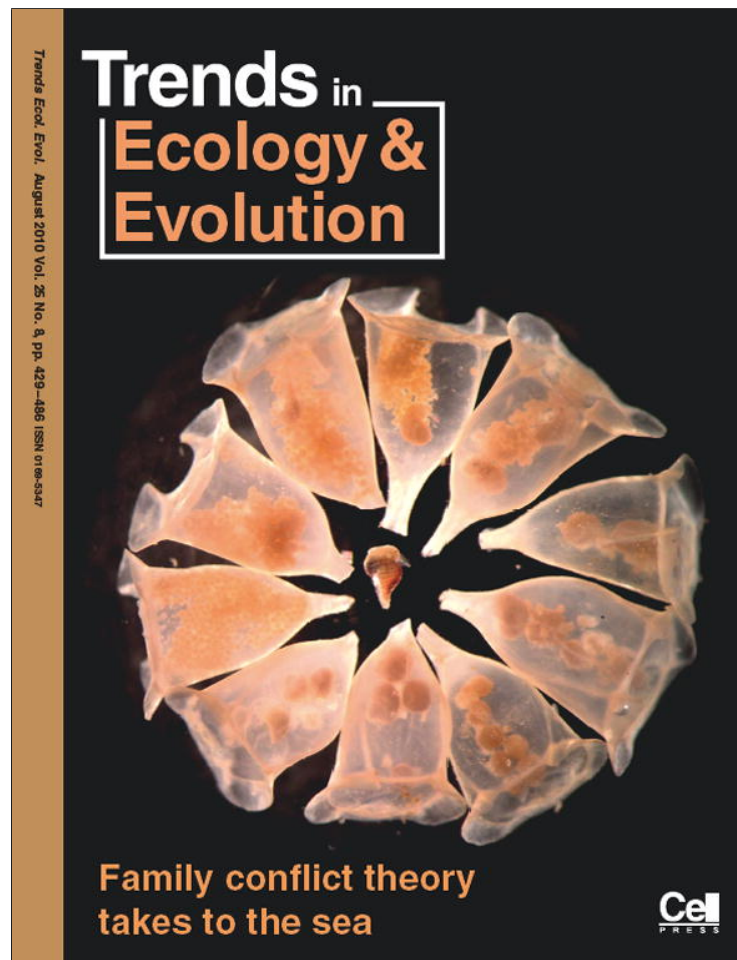


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Sexual selection: a dynamic state of affairs

Response to the comments of Cornwallis and Uller in the article: Towards an evolutionary ecology of sexual traits

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In their recent Opinion piece, Cornwallis and Uller [1] raise concerns about the current state of research on sexual selection, implying that it has "... been based on a narrow gene-centric view, leaving little room for responsive, plastic phenotypes inhabiting and creating heterogeneous environments." While we agree that environmental heterogeneity and phenotypic plasticity have critical roles in sexual selection, we do so based on ample empirical support from the literature. We argue that instead of being constrained by a lack of empirical data, progress in sexual selection research urgently requires the development of new theoretical models that better integrate existing empirical data.

We counter the sentiment expressed by Cornwallis and Uller [1] that "sexual selection studies have been based on a narrow gene-centric view" by bringing attention to the widespread support for the role of condition-dependent signaling as predicted by the Handicap model [2]. No one doubts that sexual signals result from interplay between viability and mate selection, sometimes in combination with kin selection [3], which can reinforce or oppose each other [4]. A hallmark of many sexual signals is that, despite their physiological cost, they can increase fitness *up to a point* beyond which viability selection constrains further trait exaggeration [4]. However, we increasingly encounter examples where empirical data on the dynamic nature of mating signals and choice behaviors [5] have outgrown the utility of current ecological theories for sexual signal evolution. New theory is therefore required to integrate dynamic feedbacks between environmental and genetic influences on sexual displays and the sensory and perceptual systems that govern mate choice [6].

Cornwallis and Uller [1] also raise concerns about the lack of research linking environmental heterogeneity and sexual signaling, concluding that "studies often extrapolate under the assumption that selection and the distribution of phenotypes are constant over spatial and temporal scales". While we agree that longitudinal studies linking environmental heterogeneity and sexual selection are needed at scales that go beyond within-season or inter-annual comparisons, we strongly disagree that selection and the distribution of phenotypes are typically assumed to be constant. Environmental factors clearly influence the development, display, and perception of sexual traits [e.g. 7], and sexual-

trait distributions and mate-choice decisions can vary substantially depending on environmental conditions [e.g. 8]. Cornwallis and Uller [1] also argue that "sexual traits are typically studied in isolation, but in reality reproductive success is determined by an integrated set of traits". In contrast, we note that the use of multiple sexual signals (unimodal and multimodal) and the relationship between signal evolution and environmental context have received extensive support [e.g. 9,10].

Moreover, we are surprised at the suggestion that phenotypic plasticity is all but absent from sexual selection studies. First, the argument that studies suffer from the failure to consider plasticity "as a cause of selection" is a common and unfortunate misinterpretation of the role plasticity plays in the evolutionary process. Plasticity is not a cause of natural or sexual selection [11]. Rather, plasticity changes the range of phenotypes that can be produced by a given genotype, and facilitates or constrains evolutionary change by altering the form and direction of selection acting upon heritable genetic variation [12]. Second, that "phenotypic plasticity is normally only considered in the context of condition dependence" does not appear problematic to us. Indeed, condition dependence is integral to the way in which environmental heterogeneity and genetic control interact to generate phenotypic variation in sexual signals and many other traits.

While Cornwallis and Uller acknowledge the need for more explicit theory, they place a critical emphasis on the collection of new data to incorporate phenotypic plasticity, development, and environmental heterogeneity; whereas we feel that sexual selection research has excelled in these areas. Instead, it is not primarily empirical data and methodological approaches that are lacking, but rather a strong, integrative framework to accommodate dynamic interactions between sexual and display traits, cognitive and perceptual selectivity, and social and physical environments. Advancing our understanding of sexual selection will ultimately require a revised body of theory that appropriately predicts the dynamic interplay, including environmental heterogeneity and the range of plasticity, among the diverse signaling and perceptual features of sexual signals within their ecological contexts.

Acknowledgements

RJS and MNV thank the Safran Research Team for discussion related to this letter and to NSF grant # IOS0717421 for supporting their research

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on sexual selection. MEH is supported by a grant from the Human Frontier Science Program. CKG acknowledges NSF grant #DEB0846175 for support.

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doi:10.1016/j.tree.2010.04.004 Trends in Ecology and Evolution 25 (2010) 429–430

Letters Response

Dynamic affairs—could be if we let it!

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The aim of our opinion paper was to highlight the potential importance of fluctuating selection and phenotypic plasticity in the evolution of sexual traits, topics that have been fundamental for understanding how non-sexual traits evolve [1]. Safran *et al.* [2] state that they disagree with aspects of our contribution, advocating that business should continue as usual with respect to empirical research, but what is 'urgently required' is 'the development of new theoretical models'. In our paper we tried to highlight that we think new theory is important by stating 'we need more explicit theory' in the first point of the discussion and concluding with a call for the 'joint progression of theoretical and empirical studies' [1]; it would be a shame to have new models without new data to test their predictions. It therefore seems that Safran *et al.* [2] agree more with our perspective than they disagree. However, some of Safran *et al.*'s [2] other remarks indicate to us that their perspective might perhaps obscure the development of such a theoretical framework, and so making a few additional remarks on their response might be worthwhile.

First, we proposed that a better understanding is needed of how the evolution of sexual traits is influenced by the interaction between different selection pressures (sexual, viability and kin) over space and time [1]. Safran *et al.* [2] state that 'no one doubts' this and reiterate the classic view that viability selection curbs the exaggeration of sexual traits. However, the point is not if this is theoretically possible or not (in fact, it is possible), but rather that there is relatively little research on how different selection pressures interact (beyond viability selection curbing sexual selection) and change over space and time

in populations with different genetic structures and demographics [3–5]. We are by no means the first to point this out. Recent reviews have also noted the lack of integration between research on sexual selection and other disciplines such as kin selection [6]. We raised this issue again within the context of fluctuating selection on sexual traits with the hope of generating more integrative research in the future.

Second, Safran *et al.* [2] take exception to our point that sexual traits are often studied in isolation and results are extrapolated over temporal and spatial scales. They state 'we note that the use of multiple sexual signals (unimodal and multimodal) and the relationship between signal evolution and environmental context have received extensive support'. We believe this point is best answered by a review [5] of this topic in the May 2010 issue of TREE, which states 'research [on multiple signalling]... has taken a largely static view of the world' concluding that 'Future challenges will include identifying the circumstances under which environmental fluctuations lead to multiple signalling'.

Third, Safran *et al.* [2] seem happy to see the role of phenotypic plasticity being dealt with only in terms of condition-dependence. As briefly outlined in our opinion and reviewed in more depth elsewhere [7], we believe condition-dependence does not capture the role of plasticity in the evolution of sexual traits. To illustrate this using a basic example from within the standard research framework of sexual selection, imagine a situation where all individuals are in exactly the same condition, but are placed in different social contexts, say one male with two females vs. two males with one female. Males are predicted to plastically adjust the amount of sperm they allocate to females [8], but this does not have anything to do with their condition; it could, but it doesn't have to. More

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