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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 generally, we believe that only examining plasticity from the perspective of condition dependence ignores many important and interesting aspects of plasticity, including its role in the origin of novel secondary sexual traits and its impact on the direction of evolutionary trajectories (including the evolution of condition dependent expression of sexual traits [9]) [7,10,11]. We believe examining plasticity in sexual traits more generally than just condition dependence is a more encompassing approach that will draw direct links with other areas of evolutionary ecology [10–12]. In fact, it has been noted that a proper understanding of the role of plasticity in evolution, using empirical and theoretical approaches, is considered one of the greatest challenges in evolutionary research [10–12]. Studies of sexual traits in this context might hold important insights and are well worth pursuing [7,9].

Finally, Safran *et al.* [2] disagree with our opinion by stating 'plasticity is not a cause of natural or sexual selection'. We, and others, believe it is [7,10,11]. Simply put, if organisms change their phenotype in response to environmental conditions (plasticity), this can change their interactions with other individuals. It is well recognised that biotic interactions are an important component of selection. Consequently, plasticity can cause changes in selection acting on surrounding individuals and in this sense plasticity is a cause of selection [7]. A similar effect could also be achieved if organisims change their abiotic environment [13]. In fact, Safran *et al.* [2] again probably agree more than they disagree since they state that 'plasticity facilitates or constrains evolutionary change by altering the form and direction of selection'. If plasticity alters the form and direction of selection, it seems reasonable to us to call it a cause of variation in selection.

To summarize, we reiterate our original point [1], which seems to agree in part with Safran *et al*.'s main message,

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that theory on the evolution of sexual traits should incorporate fluctuating selection and the responses of individuals to such fluctuations (phenotypic plasticity). However, in contrast to Safran *et al.* [2] we believe that studying the evolution of sexual traits purely from the traditional perspective of 'sexual selection' and developing theory without empirical input will lead to disappointment.

References

1 Cornwallis, C.K. and Uller, T. (2010) Towards an evolutionary ecology of sexual traits. *Trends. Ecol. Evol.* 25, 145–152
2 Safran, R.J. *et al.* Sexual selection: a dynamic state of affairs. *Trends. Ecol. Evol.* (in press) doi:10.1016/j.tree.2010.04.004
3 Oh, K.P. and Badyaev, A.V. (2008) Evolution of adaptation and mate choice: Parental relatedness affects expression of phenotypic variance in a natural population. *Evol. Biol.* 35, 111–124
4 Alonzo, S.H. (2010) Social and coevolutionary feedbacks between mating and parental investment. *Trends. Ecol. Evol.* 25, 99–108
5 Bro-Jørgensen, J. (2010) Dynamics of multiple signalling systems: animal communication in a world in flux. *Trends. Ecol. Evol.* 25, 292–300
6 Boomsma, J.J. (2007) Kin selection versus sexual selection: why the ends do not meet. *Curr. Biol.* 17, R673–R683
7 Price, T.D. (2006) Phenotypic plasticity, sexual selection and the evolution of colour patterns. *J. Exp. Biol.* 209, 2368–2376
8 Parker, G.A. (1998) Sperm competition and the evolution of ejaculates: Towards a theory base. In *Sperm Competition and Sexual Selection* (Birkhead, T.R. and Møller, A.P., eds), pp. 3–54, Academic Press
9 Price, T.D. *et al.* (2008) Phenotypic plasticity and the evolution of a socially selected trait following colonization of a novel environment. *Am. Nat.* 172, S49–S62
10 Pigliucci, M. (2010) Phenotypic plasticity. In *Evolution–The Extended Synthesis* (Pigliucci, M. and Müller, G.B., eds), pp. 355–379, MIT Press
11 West-Eberhard, M.J. (2003) *Developmental Plasticity and Evolution*, Oxford University Press
12 Chevin, L.M. *et al.* (2010) Adaptation, plasticity, and extinction in a changing environment: towards a predictive Theory. *PLoS Biol.* 8, 1–8
13 Lewontin, R.C. (1983) Gene, organism, and environment. In *Evolution from Molecules to Men* (Bendall, D.S., ed.), pp. 151–172, Cambridge University Press

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