

EVOLUTIONARY GENETICS

Evolution of mate choice in the wild

Arising from: A. Qvarnström, J. E. Brommer & L. Gustafsson *Nature* 441, 84–86 (2006)

Qvarnström *et al.*¹ test whether the preference of female collared flycatchers (*Ficedula albicollis*) for males with large forehead patches could have evolved as a by-product of selection acting on male patch size². They find that the crucial genetic correlation between female choice and male patch size is not significant, and conclude that preference for large patches must have been shaped directly by selection. However, their use of the patch size of a female's social partner as a measure of choice is incomplete, and will result in low estimates of the potential for direct selection to shape female preference. Their study is therefore unable to resolve the question of how female preference for large forehead patches has evolved³.

Female preference for males with exaggerated ornaments is an important source of sexual selection⁴. For example, male collared flycatchers with enlarged forehead patches pair up with a female more rapidly than do normal males⁵. To resolve the controversy over whether such preferences can evolve as a by-product of selection acting on male ornaments³, Qvarnström *et al.*¹ investigate the quantitative genetics underlying variation in female mate choice in relation to male forehead patch size. Whereas patch size is moderately heritable, the heritability of female choice is close to zero, with a non-significant genetic correlation between the two. They argue that their estimated genetic correlation from a free-living bird population provides a better test of the potential for indirect selection than the strong genetic correlations found from laboratory studies on fish⁶ and insects⁷. We challenge this view, and draw attention to important limitations in how Qvarnström *et al.* measured mate choice.

Whereas laboratory studies use the power of

experimental choice trials, Qvarnström *et al.* use the patch size of a female's social partner. Believing that a female's social partner reflects her preference assumes that the distribution of male ornament size matches the distribution of female preference, and that every female can get what she wants. (This is akin to suggesting that Angelina Jolie is the only woman who finds Brad Pitt attractive and that most women prefer overweight men.) But in species such as the collared flycatcher, males and females are effectively removed from the pool of available partners when they form socially exclusive pair bonds. However, females mated to small-patched males do regularly copulate with extra-pair males with a larger patch, accounting for 90% of the sexual selection on male patch size⁸. By ignoring this important expression of preference, Qvarnström *et al.* overlook the main evolutionary pathway by which indirect selection on preference for large patches might act.

Given that mean female choice does not differ from mean male patch size and that variation in fitness is not larger in males than in females (Table 1 in ref. 1), the measure of choice used by Qvarnström *et al.* is unable to capture variation in female preference for large forehead patches. It therefore remains unclear whether variation in female preference affects which males females pair up with.

We agree with Qvarnström *et al.*¹ that partnership formation is shaped by a range of ecological processes, if only because not every female can partner with her preferred male. However, this reduces the importance of female preference in partnership formation *per se*, and determines both her indirect and direct fitness. The potential for both indirect and direct selection to shape the evolution of

preference is therefore, absolutely speaking, low. The issue about their relative importance cannot be settled until the potential for direct selection is quantified, and both are compared directly⁹. A non-significant genetic correlation between ornament and choice (between -0.3 and 0.3), and a significant heritability of choice (of $0.01-0.04$) is not sufficient to support the argument.

Instead of dismissing results from the laboratory as unnatural, or from long-term wild data sets as unreplicated and correlational, we should study classic laboratory species in the wild and wild animals in captivity. This will allow for careful estimation of genetic variances and covariances of the appropriate traits, and thereby, for meaningful tests of evolutionary models of sexual selection¹⁰.

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We have shown¹ that there is little scope for selection on male flycatchers' forehead patch size to drive the evolution of female choice for this ornament indirectly. Postma *et al.*² question this conclusion, arguing that a female's social partner (that is, realized mate choice) is not a good estimate of her preference, and that our estimates are biased because we do not take patterns of extra-pair paternity into account. However, indirect sexual selection can only operate through realized mate choice, and extra-pair copulations are associated with larger costs than indirect benefits.

Postma *et al.*² confuse the phenotypic and the genetic processes underlying indirect selection on mate choice. First, our use of mate choice is justified by the focus of models of indirect sexual selection on the heritability of realized preferences (that is, mate choice) and their assumption that a genetic correlation between ornament and choice is built up and maintained through a phenotypic correlation between mated pairs. A correlation between preference (unconstrained propensity to mate with a partner with a particularly sized ornament) and mate choice (its realized equivalent)

has been explicitly specified³, because preferences that are never realized cannot be exposed to selection, nor can their genes become associated with male genes for ornamentation. The point of Postma *et al.* that every female does not get what she wants in wild populations therefore underlines our conclusion of low potential for indirect sexual selection, rather than challenges it.

Second, the question is not whether one actress is the only person to find an actor attractive. It is whether her female relatives (who share her genes) make a mate choice that