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## Sexual Selection: Does Condition Dependence Fail to Resolve the ‘Lek Paradox’?

The ‘lek paradox’ — the hypothesis that females do not gain substantial genetic benefits from mate choice — could be resolved by sexually selected traits being indicative of male condition. A recent paper, however, suggests that this may not be the case in *Drosophila bunnanda*.

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One of the longest running and most contentious issues in the study of sexual selection is the degree to which elaborate male ornaments — and female preferences for them — confer a genetic fitness advantage. Male sexual traits are expected *a priori* to harbour little genetic variance, as the strong selection they encounter due to directional mate preference quickly drives favoured alleles to fixation, thereby depleting heritable variation [1,2]. This has given rise to the ‘lek paradox’: why do females, who receive only genes during mating, continue to discriminate between males if there are so few genetic benefits of choice [3,4]?

The most persuasive resolution to this problem in evolutionary biology comes from the expectation that sexual ornaments are expressed in proportion to male genetic condition, as only high quality individuals are expected to be able to afford to ‘pay the price’ of possessing such costly traits [5]. Condition is defined as a trait showing strong covariance with general viability,

such that higher trait values confer greater fitness. Many loci are expected to affect condition, and hence condition should provide a broad target for intrinsic (e.g. mutations) and extrinsic (e.g. parasites, stress) factors that counter the depletion of genetic variance through selection [6]. Empirical support for this hypothesis comes from the observation that sexually selected traits tend to show heightened condition-dependent expression [7], often covary positively with male viability [8] and typically display high levels of genetic variation [9].

In an intriguing new study published in *Current Biology*, Van Homrigh *et al.* [10] examine the model of condition-dependent ornaments as a resolution of the lek paradox in a species in which females exhibit mate preference for complex male traits. Male *Drosophila bunnanda* (Figure 1), and other members of the *Drosophila serrata* species complex, emit cuticular hydrocarbons (CHCs) that are important cues used by females in mate choice decisions. Male CHC blends are highly dimensional — in *D. bunnanda*

nine different molecules define the sexual trait [10]. This complexity stands in marked contrast to many of the ‘simpler’ ornaments often studied in sexual selection, which tend to be measured on one or at most a few axes of variation, such as tail length or song amplitude. Van Homrigh *et al.* [10] asked three questions: do CHCs, individually and collectively, exhibit genetic variance? Is there any genetic covariance between CHCs and a component of male condition, body size? Does female choice act on CHCs in such a way that it selects indirectly for genetic variation in CHCs and male condition? The last question is particularly important in systems with multiple sexually selected traits, as there are many dimensions on which females can select; if there is little genetic (co-) variation of CHCs with condition parallel to the direction of female preference, then there will be no genetic advantage for choosy females. Van Homrigh *et al.* [10] found that all of the nine individual CHCs studied showed high levels of genetic variation. In addition, genetic variance in the nine CHCs accounted for almost 20% of the heritable variation in body size, suggesting a strong and informative genetic link (covariance) between these sexually selected traits and condition.

Van Homrigh *et al.* [10] then asked whether females actually preferred combinations of CHCs that were revealing in terms of male condition. Females were found to prefer relatively high concentrations of certain CHCs but



Figure 1. Resurrecting the 'lek paradox'?

A mating pair of *Drosophila bunnanda*. Does sexual selection on cuticular hydrocarbons in this species create a complex bouquet of problems for sexual selection theory? (Photograph courtesy of Anna Van Homrigh.)

lower concentrations of others. To understand how this affects the genetic benefits of mate choice, Van Homrigh *et al.* [10] showed that the complex genetic variation and covariation between the nine individual CHCs could be almost entirely accounted for by five independent (multi-dimensional) genetic axes. When these five uncorrelated genetic dimensions were compared with the measure of mate preference, the amount of genetic variation in the direction of sexual selection was found to be negligible. This means that females will gain little or no genetic benefit from their mate choice and might as well have mated at random. These results lead the authors to suggest that sexual selection in multi-trait (as opposed to single-trait) systems will deplete genetic variation along its axis of action, and that condition dependence is insufficient to overcome the erosion of heritable variation in fitness. Does this mean that the 'lek paradox' has been resurrected?

Van Homrigh *et al.* [10] use a multivariate quantitative genetic approach, and the pros and cons of this have been discussed elsewhere [11]. The response to selection predicted by these authors requires that the genetic variances and covariances of CHCs do not change over time or vary under natural conditions [12]. A number of studies suggest that this assumption is unrealistic for sexual traits, as the environment has a large influence on the amount and covariation of the genetic terms [13–16]. Heritable variation available for sexual selection might, therefore, only become manifest in certain environments, and hence 'adaptive' female choice

may only be detectable in a subset of situations.

In particular, genetic variance in sexually selected traits is predicted to be highest in harsh environments, as these tend to reveal and amplify differences between individuals with respect to quality [7,14]. Van Homrigh *et al.*'s study [10] was, however, performed in a single, benign laboratory environment that may have masked genetic differences between males. It would be extremely interesting to view the results of the same experiment conducted over a gradient of environmental change, to see if genetic variation in CHCs increases with stress in the multi-dimension axis subject to mate choice.

A second problem is that only one component of condition, body size, was investigated. Body size is used as an index of condition with monotonous regularity in the sexual selection literature, yet there are scores of other fitness and viability traits that are unrelated to body size and that could equally be given the moniker of 'condition'. If females really wanted to mate with larger males, surely it would be easier for them to use simple visual cues rather than complex olfactory ones? Or are there reasons why visual cues are unavailable to female *D. bunnanda*? Body size is often used as a measure of 'condition' for the simple reason that it is easy to measure, and seems a reasonable proxy for other fitness traits, such as longevity or fertility. But this can't be assumed, it needs to be established. Insight would be gained by showing whether sexually preferred CHC blends are genetically correlated with a suite of fitness traits — and

this ideally needs to be done under field conditions, rather than unnatural laboratory conditions.

Finally, the generality of Van Homrigh *et al.*'s [10] results needs to be addressed. Mate choice in *D. bunnanda* is based on cuticular hydrocarbons which can only be studied using multi-dimension measurements of CHC components. This forced the authors to adopt multi-variate statistical analyses. But are their conclusions likely to be limited to complex traits? Other sexual traits appear to be far simpler and uni-variate measurement and analyses have usually proved adequate, such as tail length in widow birds, [17] or eyespan in stalk-eyed flies, [18]. However, sexual display in these other species typically contains many complexities (e.g. calls, jump flights, dance rings in the widow bird), so there is no clear distinction to draw.

So do we expect many sexual displays to show a similar lack of genetic variation in the direction of mate choice once appropriate multi-variate measurements are made? We suggest not. The important lesson to learn from Van Homrigh *et al.*'s study [10] is that all traits contributing to male display need to be taken into account. We predict some traits (or independent genetic axes) will show genetic variation and others will lack genetic variation. Even Van Homrigh *et al.*'s study [10] suffers from this problem. They measured variation in the relative concentration of CHC components but ignored variation in the absolute quantity of CHCs produced. As the former accounts for only about 10% of the variation in mate choice, we suspect an influence of absolute quantity of CHCs on mate choice. Perhaps these other dimensions will show higher levels of genetic variation? In addition, the strength and direction of sexual selection was computed under a narrow set of experimental conditions (female choice between two males in a Petri dish). Estimates of mate preference are well known to be highly contingent on the environment and the way preference is assayed [19,20].

More ecologically realistic measures of sexual selection are needed. There seems no easy way to overcome these issues without further empirical work to assess the generality of the claim to have revived the lek paradox.

In spite of these few problems, Van Homrigh *et al.*'s [10] study represents a major challenge to the way we view the forces and consequences of sexual selection. 'Resolutions' of the lek paradox [6,9] need to be examined again, in particular with more in depth quantitative genetic and fitness measures. This needs to be followed up by the mapping of the individual loci involved and quantification of their contribution to genetic variation between males.

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