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SEXUAL CONFLICT AND THE MAINTENANCE OF MULTIVARIATE GENETIC VARIATION

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Mate choice should erode additive genetic variation in sexual displays, yet these traits often harbor substantial genetic variation. Nevertheless, recent developments in quantitative genetics have suggested that multivariate genetic variation in the combinations of traits under selection may still be depleted. Accordingly, the erosion and maintenance of variation may only be detectable by studying whole suites of traits. One potential process favoring the maintenance of genetic variance in multiple trait combinations is the modification of sexual selection via sexually antagonistic interactions between males and females. Here we consider how interlocus sexual conflict can shape the genetic architecture of male sexual traits in the cricket, *Teleogryllus commodus.* In this species, the ability of each sex to manipulate insemination success significantly alters the selection acting on male courtship call properties. Using a quantitative genetic breeding design we estimated the additive genetic variation in these traits and then predicted the change in variation due to previously documented patterns of sexual selection. Our results indicate that female choice should indeed deplete multivariate genetic variance, but that sexual conflict over insemination success may oppose this loss of variance. We suggest that changes in the direction of selection due to sexually antagonistic interactions will be an important and potentially widespread factor in maintaining multivariate genetic variation.

KEY WORDS: Crickets, harassment, interlocus conflict, lek paradox, quantitative genetics, sexual selection.

The maintenance of genetic variation in traits that are under selection remains the most persistent and controversial problem in evolutionary biology (Barton and Turelli 1989; Tomkins et al. 2004; Johnson and Barton 2005). This is particularly true for sexual displays because genetic variance in these traits also underpins any potential for genetic benefits of mate choice, giving rise to the lek paradox (Kirkpatrick and Ryan 1991; Kotiaho et al. 2001). However, although empirical research to date has been successful in documenting the amount of genetic variation in single traits (Pomiankowski and Møller 1995) and demonstrating how this variation may be maintained (Tomkins et al. 2004; Kotiaho et al. 2008; Radwan 2008), recent developments in quantitative genetics suggest that genetic variation may still be depleted along the major multivariate combinations of traits under selection (Hine et al. 2004; Hunt et al. 2007; Van Homrigh et al. 2007). Moreover, the effectiveness of mechanisms that can maintain genetic

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variation in single traits, such as condition dependence, have recently been questioned when the multivariate genetic variation in the suite of traits under selection has been considered (Cotton and Pomiankowski 2007; Van Homrigh et al. 2007). To resolve this newly derived "multivariate lek paradox," it is important to identify processes that may maintain genetic variation in the entire multivariate suite of traits.

One potential process favoring the maintenance of genetic variance in multiple trait combinations is the modification of sexual selection via sexually antagonistic interactions between males and females. However, although sexual conflict is increasingly recognized as an important evolutionary force (Hosken and Snook 2005; Chapman 2006), the evidence that sexual conflict affects the maintenance of genetic variance in traits under selection has so far been restricted to the role of intralocus sexual conflict due to sexually antagonistic genes (Pischedda and Chippindale 2006; Foerster et al. 2007). Interlocus sexual conflict, including antagonistic interactions between males and females over mating, can also potentially contribute to the maintenance of genetic variance (Candolin 2004; Hall et al. 2008), but we are not aware of any studies that have attempted to address this idea. This lack of attention is surprising given that antagonistic interactions between males and females are highly likely to change the direction and intensity of sexual selection (Parker 2006). As theory has already identified changes in the form of selection as a powerful process opposing the erosion of genetic variation (Sasaki and Ellner 1997; Reinhold 2000), interlocus sexual conflict constitutes a potentially widespread mechanism for the maintenance of genetic variation in sexual signals.

Here we consider how interlocus sexual conflict is likely to shape the multivariate genetic architecture of the male courtship call in the cricket, *Teleogryllus commodus.* In this species, sexual conflict occurs over the attachment duration of an external spermatophore following copulation, with both sexes attempting to manipulate attachment times to their advantage. For females, the timing of the spermatophore removal is a form of postcopulatory choice that biases insemination success in favor of the attractive males and thus reinforces precopulatory choice (Bussière et al. 2006; Hall et al., in prep). Following copulation, however, males vigorously harass females to delay spermatophore removal (Loher and Rence 1978; Evans 1988) and thus manipulate their own insemination success. Importantly, unlike other species of cricket where male harassment may potentially indicate the condition or quality of the male (e.g., Zuk 1987), in *T. commodus* it is the poor quality, unattractive males who harass females the most intensely and who benefit the most from this behavior (Bussière et al. 2006). This has led to the suggestion that by constraining the ability of females to exercise choice, sexual conflict over spermatophore removal will have important consequences for the combinations of male traits favored by sexual selection (Bussière et al. 2006; Hall et al. 2008).

In *T. commodus* and many other cricket species the properties of the courtship call (see Fig. 1) and the size of the male are important determinants of mating success (Simmons 1986; Balakrishnan and Pollack 1996; Tregenza et al. 2006). In a previous study, Hall et al. (2008) showed how the ability of males and females to influence spermatophore attachment significantly changes the form and intensity of sexual selection acting on these sexual traits. When males are unable to harass females and females can thus exercise uninhibited postcopulatory choice, the dominant pattern of selection describes a multivariate stabilizing peak, where virtually all male trait combinations are under this variance-reducing form of selection (figure 3 of Hall et al. 2008). In contrast, when males are able to harass females to delay spermatophore removal, the pattern of selection changes dramatically and becomes dominated by disruptive selection occurring along a combination of courtship call properties and body size (figure 2 of Hall et al. 2008). Based on these simple contrasting patterns
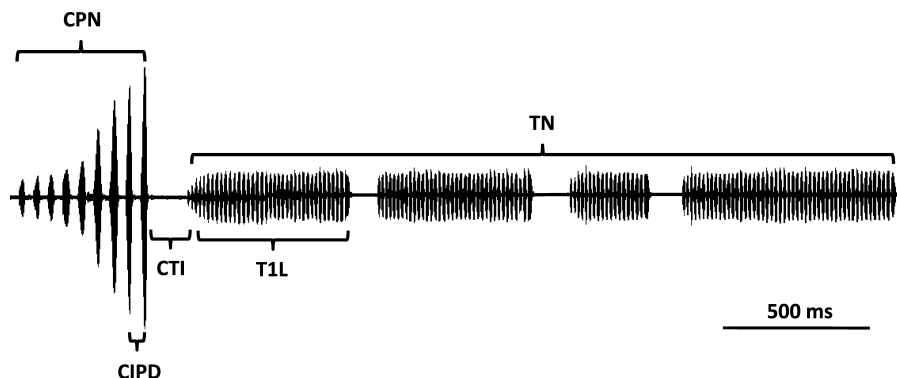

Figure 1. The courtship call of *Teleogryllus commodus* as previously presented in Hall et al. (2008). The waveform diagram shows a single amplitude-modulated chirp sequence followed by a longer trill sequence of consistent intensity. We measured the number of pulses in the chirp (CPN), the duration of the interval between last pulses in the chirp (CIPD), the interval between the chirp and trill (CTI), the length of the first trill sequence (T1L), the number of trills (TN), and the dominant frequency (DF, not shown).

of strongest selection (stabilizing vs. disruptive) we might expect that genetic variance would be more likely to be depleted by female choice and likewise to increase as a consequence of male harassment. However, the uninhibited postcopulatory female choice treatment also yielded a multivariate combination of male traits under weak, but significant disruptive selection, whereas the male harassment treatment was additionally characterized by two multivariate combinations of traits under stabilizing selection. Even these minor patterns of selection may still be important if they are occurring in a direction of high genetic variation (Blows 2007).

Although several authors have asserted that female choice should deplete genetic variance (Kirkpatrick and Ryan 1991; Tomkins et al. 2004; Blows 2007), and a handful of studies have indicated that sexual conflict can potentially alter selection (Candolin 2004; Parker 2006; Hall et al. 2008), few studies have quantified the multivariate genetic consequences of changes in sexual selection. Importantly, the consequences for genetic variance cannot be inferred from selection alone because they depend on the interaction between multivariate selection and the underlying genetic architecture (Blows 2007). The first studies combining genetic architecture with multivariate selection estimates have shown there is typically low genetic variance in the combinations of traits under strong sexual selection (Hunt et al. 2007; Van Homrigh et al. 2007). Therefore, to evaluate the potential for genetic variation to be depleted by female choice or maintained via sexual conflict, it is necessary to consider the orientation of the two contrasting patterns of selection with the underlying genetic architecture of male sexual traits.

In this study, we present the results from a quantitative genetic experiment quantifying the genetic architecture of the *T. commodus* male courtship call and body size. We use equations of multivariate genetic change (Lande and Arnold 1983; Phillips and Arnold 1989) to combine using matrix algebra our estimates of genetic architecture with previous estimates of selection on males taken from the same source population of crickets raised under common environmental conditions (Hall et al. 2008, but see methods below for more details). We first apply estimates of selection due to female choice alone to test how the patterns of selection due to choice are aligned with the genetic architecture of the male sexual display traits. Based on this finding, we formally predict whether female choice is expected to deplete genetic variance in all multivariate combinations of the male traits. We then apply estimates of selection under conditions that heighten male–female conflict over insemination to predict if interlocus sexual conflict can change the association between selection and the genetic architecture of male displays, and whether conflict can potentially oppose the loss of genetic variance that is due to choice.

Methods

To predict the potential for sexual conflict to shape the genetic architecture of male sexual traits, we first reared crickets as part of a quantitative genetic breeding design and measured the courtship call characteristics and body size of multiple males per full-sib family. The parental animals for this experiment originated from the fourth generation offspring of a laboratory culture of *T. commodus*, collected from Smiths Lake (32°22′S, 152°30′E), New South Wales, Australia. We then described the multivariate genetic architecture of the male sexual traits by estimating the additive genetic variance–covariance matrixes (**G**) for the six courtship call characteristics and body size. Finally, we integrated our newly derived estimates for the genetic architecture of male sexual traits with the two contrasting patterns of selection that have been documented previously in Hall et al. (2008): one where females could exhibit uninhibited postcopulatory choice, and another where males were able to harass females. We describe each of these experimental aspects below in more detail.

QUANTITATIVE GENETIC EXPERIMENT

Using a standard half-sib breeding design we mated 54 sires each to six dams each. This resulted in 237 full-sib families as nine males died before completing the six matings and 43 dams failed to produce any offspring. From each half-sib family, we measured the weight and pronotum width at eclosion of males who had been raised individually since hatching. From these two measures, we extracted a single principal component that described 90% of variation in cricket body size. At 12 to 14 days posteclosion, males were then placed together with a female in a small plastic container ($7 \times 7 \times 5$ cm) to induce calling. We then recorded the calls as uncompressed audio using a Sony Hi-MD walkman (MZ-NH700, Sony, Japan) connected to a condenser microphone (C1163, Dick Smith Electronics, Chullora, NSW, Australia), which was mounted in the lid of the container. To power the microphone a junction unit was used between the microphone and recorder. Using the Raven sound analysis software (version 1.2, Cornell Bioacoustics Research Program, Ithaca, NY), we measured the six call properties used in previous studies (see Fig. 1), for five randomly selected calls per male. We used the averages of the five calls as our estimates for the call properties in the genetic analyses. In total, the calls of 865 males were recorded and analyzed.

GENETIC ANALYSES

We used a multivariate model to estimate the seven-dimensional additive genetic variance–covariance (**G**) matrix as implemented in the MIXED procedure of SAS (Version 9.1: SAS Institute Inc, Cary, NC). Restricted maximum likelihood was used to estimate the variance components as part of a standard half-sib nested model. We transformed CPN and TN using natural logarithms

and CIPD and CTI using square root transformations, before standardizing all traits to a mean of zero and a standard deviation of one. Factor-analytic modeling of **G** (Hine and Blows 2006) was conducted by sequentially dropping a dimension from a factor analytic model at the sire level implemented in the MIXED procedure. A series of nested log likelihood ratio tests were used to determine when the dropping of a dimension resulted in a significantly worse fit and therefore, the statistical support for the presence of the dropped dimension.

SELECTION ESTIMATES

Our estimates for the contrasting patterns of selection based on female choice only or under heightened male–female conflict have been previously described in Hall et al. (2008). In that study, Hall et al. (2008) used the same source population of crickets as those used here for the quantitative genetic design, and created two experimental treatments which manipulated the balance of sexual conflict through a series of behavioral trials. In one treatment, females were allowed to exercise postcopulatory spermatophore removal uninhibited (the female only treatment), whereas in the other treatment, males could freely harass the females (the male present treatment). Formal selection analysis (Lande and Arnold 1983) and response surface comparisons (Blows and Brooks 2003; Chenoweth and Blows 2005) were then applied to estimate and statistically compare the multivariate fitness surfaces in each treatment. In all cases, spermatophore attachment duration was the dependent variable (i.e., the estimate of fitness) and male courtship call properties and body size were the independent variables. In this way, the vector of standardized linear selection gradients (β) and the matrix of standardized quadratic and correlational selection gradients (γ) were estimated (see Lande and Arnold 1983 for formal definitions of these standardized gradients). Our analyses for this study are based on these linear (β) and nonlinear (γ) selection gradients. In both behavioral treatments, there was no significant evidence for linear selection acting on the male courtship call and body size. Instead, the variation in the duration

of spermatophore attachment was associated with strong nonlinear selection and this selection differed significantly between the female only and male present treatments. We therefore do not further refer to the effects of linear selection, although where appropriate these estimates are used in the equations of evolutionary change. Further methodological details and results are presented in Hall et al. (2008), particularly Table 2 therein.

Results

To resolve the effects of each selective context on the genetic variance in the six courtship call properties and body size, we first estimated the additive genetic variance–covariance (**G**) matrix (Table 1) and then used factor-analytic modeling (Hine and Blows 2006) to assess the dimensionality of **G** and test which parts of the genetic subspace had statistical support (Table 2). We found strong statistical support for the presence of three genetic dimensions accounting for 81.5% of the estimated genetic variance (log-likelihood ratio test: $\chi^2 = 11.8$, df $= 5$, $P = 0.038$). The first eigenvector of **G**, known as g_{max}, contrasted body size and call dominant frequency with the other courtship call properties and explained 33.5% of the estimated genetic variance. The second and third eigenvectors, g_2 and g_3, reflect the remaining contrasts between the various call properties and body size, and explained 25.5 and 22.5% of the estimated genetic variance, respectively.

For both experimental situations (female choice only, or heightened male–female conflict), we estimated using equations of multivariate evolutionary change the strength of non-linear sexual selection along each of the genetic eigenvectors of male traits as $g_n^T \gamma g_n$, where **T** denotes matrix transposition (after Lande 1980; Lande and Arnold 1983). We then predicted the change in genetic variance along each eigenvector of **G** using $g_n^T \Delta G g_n$, where the within-generation change in **G** from a single generation of selection is given by $\Delta G = G(\gamma - \beta\beta^T)G$ (Lande and Arnold 1983; Phillips and Arnold 1989). When females were allowed to exercise postcopulatory choice unhindered, stabilizing selection

Table 1. The additive genetic variance–covariance (G) matrix of courtship call properties and body size for *T. commodus*. The genetic variances of standardized traits (equivalent to heritabilities) are along the diagonal and the genetic covariances are below the diagonal. The courtship call properties represented include: chirp pulse number (CPN); chirp interpulse duration (CIPD); chirp to trill interval (CTI); first trill length (T1L); trill number (TN); and dominant frequency (DF).

	CPN	CIPD	CTI	T1L	TN	DF	Body size
CPN	0.451						
CIPD	0.081	0.160					
CTI	−0.044	0.015	0.207				
T1L	0.066	−0.057	−0.007	0.060			
TN	0.113	0.038	0.163	−0.011	0.321		
DF	−0.038	−0.048	0.028	0.035	0.034	0.277	
Body size	−0.068	0.105	−0.030	−0.046	0.042	−0.078	0.137

Table 2. The eigenvectors and eigenvalues (λ_n) of G. The strength of nonlinear selection along each eigenvector is given by $g_n^T \gamma\, g_n$ and the predicted response of the genetic variation to selection along each eigenvector is given by $g_n^T \Delta G\, g_n$.

	g_{max}	g_2	g_3	g_4	g_5	g_6	g_7
CPN	0.802	−0.442	0.219	0.025	0.080	−0.026	−0.324
CIPD	0.212	−0.067	−0.432	0.509	0.512	0.103	0.482
CTI	0.156	0.577	−0.067	−0.349	0.585	0.228	−0.349
T1L	0.069	−0.065	0.281	−0.143	−0.148	0.870	0.335
TN	0.528	0.573	−0.156	−0.033	−0.500	−0.157	0.306
DF	−0.049	0.366	0.607	0.686	0.037	0.012	−0.149
Body size	−0.035	0.015	−0.537	0.355	−0.342	0.393	−0.560
λ_n	0.549	0.418	0.370	0.177	0.095	0.031	−0.028
% var	33.5	25.5	22.5	10.8	5.8	1.9	0
Selection based on female control							
$g_n^T \gamma\, g_n$	−0.089	−0.265	−0.003	−0.092	−0.526	−0.230	−0.158
$g_n^T \Delta G\, g_n$	−0.029374	−0.047741	−0.000375	−0.002872	−0.004786	−0.000220	−0.000126
Selection based on male harassment							
$g_n^T \gamma\, g_n$	0.011	0.055	−0.021	0.070	−0.091	0.003	0.029
$g_n^T \Delta G\, g_n$	0.003265	0.009625	−0.002911	0.002187	−0.000843	0.000003	0.000023

occurred along each of the seven eigenvectors of **G**. Moreover, genetic variance was predicted to decrease along all major genetic dimensions, with the strongest reduction in variance predicted to occur along the two major dimensions of **G** (g_{max} and g_2). In contrast, when males were able to harass females five of the seven genetic dimensions were subjected to disruptive selection. Our findings therefore predict an increase in the genetic variance in male courtship call properties and body size along these five out of the seven multivariate genetic dimensions, including the two major genetic dimensions of **G** (g_{max} and g_2) that account for nearly 60% of the total estimated variance in male sexual traits.

These results suggest that in general female choice should deplete genetic variation as a result of stabilizing selection and that male harassment should instead increase genetic variation due to disruptive selection. To assess the robustness of these findings, we first use the statistical support associated with each of the genetic dimensions. As discussed above, the factor-analytic modeling of **G** indicated strong statistical support for the presence of three genetic dimensions (g_{max}, g_2 and g_3) and thus suggests that the most important and robust differences in selection are those that occur along these genetic dimensions. Second, we assess the strength of the nonlinear selection occurring along each of the statistically supported genetic dimensions. In the case of selection based on female control, the confidence intervals for selection occurring along each eigenvector give strong support for significant selection along g_{max} (95% CI: −0.006, −0.173) and g_2 (95% CI: −0.202, −0.327), but not for g_3 where the confidence intervals overlap with zero (95% CI: 0.076, −0.081). In contrast for the case of selection based on male harassment, we have strong support for selection occurring along g_2 (95% CI: 0.079, 0.031), but selection along both g_{max} (95% CI: 0.043, −0.021) and g_3

(95% CI: 0.009, −0.051) appears to be weak and not significant. Nevertheless, given the significant amount of genetic variation explained by g_{max} and g_2, together with either the weakening of selection along g_{max} or a direct change in the direction of selection along g_2 that is due to male harassment, we can be confident that antagonistic interactions over spermatophore attachment will have important consequences for almost 60% of the estimated genetic variation in male courtship call and body size.

Discussion

A key prediction of sexual selection theory is that female choice erodes additive genetic variation in male sexual traits, yet few studies have tested whether such erosion is occurring and the circumstances under which it occurs. Fewer still have generated quantitative predictions of the magnitude of reduction in genetic variance. Instead, evidence that female choice depletes genetic variation comes from the lack of observed evolutionary change over multiple generations in laboratory (Hall et al. 2004; McGuigan et al. 2008) and field studies (Kruuk et al. 2002), or the lack of multivariate genetic variation in the direction of selection (Hine et al. 2004; Van Homrigh et al. 2007). Our findings indicate that the postcopulatory sexual selection (Hall et al. 2008) exerted by females in *T. commodus* should reduce the additive genetic variance in male sexual traits in at least the two major dimensions of genetic variation (g_{max} and g_2) in male courtship calls and body size. These results reinforce the multivariate nature of the lek paradox, as without processes to maintain genetic variation in the suite of traits under sexual selection, we predict that female choice will erode additive genetic variation in the multivariate combinations of male sexual traits that contribute to these

genetic dimensions. We have also shown, however, that sexually antagonistic interactions over postcopulatory reproductive interactions may potentially oppose the depletion in genetic variance that occurs due to choice. In the two major dimensions of genetic variance, selection due to male harassment is either greatly reduced resulting in little change in genetic variation (g_{max}), or is directly opposed to that driven by female choice and instead acts to increase genetic variation (g_2).

Our findings highlight interlocus sexual conflict as a potentially important factor in the maintenance of genetic variance (Kirkpatrick and Ryan 1991; Tomkins et al. 2004; Johnson and Barton 2005). If the two contrasting patterns of selection generated by sexual conflict over spermatophore attachment capture the full range of normal patterns of selection, then the existence here of substantial genetic variation in the presence of strong stabilizing selection due to postcopulatory female choice (see Table 2) would suggest that the level of male harassment in this population might have been substantial. In the field, however, a range of processes will contribute to this maintenance of genetic variation and the frequency of harassment in the population will determine the extent to which genetic variance is maintained in male courtship call characteristics and body size as a result of sexual conflict. Previous studies, for example, have suggested that opportunities for males to harass females will depend on the complexity of the environment or the availability of alternate mates (Bateman and MacFadyen 1999). These results lead to the seemingly paradoxical conclusion that by constraining individual female mating decisions, male harassment may actually increase the potential genetic benefits to choosy females in the wider population over time by increasing genetic variance.

Although for *T. commodus* there appears to be a tension between the erosion of genetic variance in male call properties by female choice and the maintenance of such variance when males are able to harass females following copulation, how these contrasting patterns of selection impact on the variety of other sexual signals in this species remains unclear. One of the ongoing challenges for quantitative genetic studies is to integrate estimates of multivariate estimates of selection and genetic architecture across multiple episodes of selection (Hunt et al. 2009). In *T. commodus*, for example, males first use a long-distance advertisement call to attract females, before switching to the close-contact courtship call to entice mating (Loher and Rence 1978; Brooks et al. 2005; Bentsen et al. 2006; Hall et al. 2008). Although data are available for estimates of selection and genetics for both types of call in *T. commodus* (here and Hunt et al. 2007), we are currently unable to integrate the two studies at the present time for two reasons: first, both call were not measured on the same groups of crickets; and second, one of the limitations of quantitative genetic studies is that the analyses are sensitive to the addition or removal of any variables (Pigliucci 2006), particularly in this system where the patterns of selection are strongly dependent on the non-linear interactions between traits (Bentsen et al. 2006; Hall et al. 2008). Nevertheless, it is important to note that by constraining the ability of females to exercise postcopulatory choice, male harassment will potentially influence the maintenance of additive genetic variation for any trait that covaries with spermatophore attachment, including traits unmeasured in this study such as advertisement call properties, morphology, or contact pheromones.

Finally, although in this study we have focused on the nature of interlocus sexual conflict in terms of variation in male insemination success, we suggest that other manifestations of sexual conflict such as the direct physical costs imposed on females (Hotzy and Arnqvist 2009), together with the chemical manipulation of female remating behavior (Chapman et al. 1995; Wigby and Chapman 2005) will also be responsible for changing the strength and form of sexual selection. In the same way, therefore, that genetic variation has been predicted to be maintained due to factors such as environmental heterogeneity (Gibbs and Grant 1987; Robinson et al. 2008) and plasticity in female choice (Chaine and Lyon 2008), the antagonistic interactions between males and females over mating (Candolin 2004; Hall et al. 2008) provide another potential process responsible for the heterogeneity of sexual selection through time and space. Progress now depends on broadening investigations of the evolutionary consequences of sexual conflict to include the genetic architecture and evolutionary change in a range of male traits, not just those that are sexually antagonistic.

LITERATURE CITED

Balakrishnan, R., and G. S. Pollack. 1996. Recognition of courtship song in the field cricket, *Teleogryllus oceanicus*. Anim. Behav. 51:353–366.

Barton, N. H., and M. Turelli. 1989. Evolutionary quantitative genetics: how little do we know? Annu. Rev. Genet. 23:337–370.

Bateman, P. W., and D. N. MacFadyen. 1999. Mate guarding in the cricket *Gryllodes sigillatus*: influence of multiple potential partners. Ethology 105:949–957.

Bentsen, C. L., J. Hunt, M. D. Jennions, and R. Brooks. 2006. Complex multivariate sexual selection on male acoustic signaling in a wild population of *Teleogryllus commodus*. Am. Nat. 167:102–116.

Blows, M. W. 2007. A tale of two matrices: multivariate approaches in evolutionary biology. J. Evol. Biol. 20:1–8.

Blows, M. W., and R. Brooks. 2003. Measuring nonlinear selection. Am. Nat. 162:815–820.

Brooks, R., J. Hunt, M. W. Blows, M. J. Smith, L. F. Bussière, and M. D. Jennions. 2005. Experimental evidence for multivariate stabilizing sexual selection. Evolution 59:871–880.

Bussière, L. F., J. Hunt, M. D. Jennions, and R. Brooks. 2006. Sexual conflict and cryptic female choice in the black field cricket, *Teleogryllus commodus*. Evolution 60:792–800.

Candolin, U. 2004. Opposing selection on a sexually dimorphic trait through female choice and male competition in a water boatman. Evolution 58:1861–1864.

Chaine, A. S., and B. E. Lyon. 2008. Adaptive plasticity in female mate choice dampens sexual selection on male ornaments in the lark bunting. Science 319:459–462.

Chapman, T. 2006. Evolutionary conflicts of interest between males and females. Curr. Biol. 16:R744–R754.

Chapman, T., L. F. Liddle, J. M. Kalb, M. F. Wolfner, and L. Partridge. 1995. Cost of mating in *Drosophila melanogaster* females is mediated by male accessory-gland products. Nature 373:241–244.

Chenoweth, S. F., and M. W. Blows. 2005. Contrasting mutual sexual selection on homologous signal traits in Drosophila serrata. Am. Nat. 165:281–289.

Cotton, S., and A. Pomiankowski. 2007. Sexual selection: does condition dependence fail to resolve the 'lek paradox'? Curr. Biol. 17:R335–R337.

Evans, A. R. 1988. Mating systems and reproductive strategies in 3 Australian gryllid crickets: *Bobilla victoriae* Otte, *Balamara gidya* Otte and *Teleogryllus commodus* Walker (Orthoptera, Gryllidae: Nemobiinae; Trigonidiinae; Gryllinae). Ethology 78:21–52.

Foerster, K., T. Coulson, B. C. Sheldon, J. M. Pemberton, T. H. Clutton-Brock, and L. E. B. Kruuk. 2007. Sexually antagonistic genetic variation for fitness in red deer. Nature 447:1107–U1109.

Gibbs, H. L., and P. R. Grant. 1987. Oscillating selection on Darwin's finches. Nature 327:511–513.

Hall, M. D., A. K. Lindholm, and R. Brooks. 2004. Direct selection on male attractiveness and female preference fails to produce a response. BMC Evol. Biol. 4.

Hall, M. D., L. F. Bussière, J. Hunt, and R. Brooks. 2008. Experimental evidence that sexual conflict influences the opportunity, form and intensity of sexual selection. Evolution 62:2305–2315.

Hall, M. D., L. F. Bussière, M. Demont, P. I. Ward, and R. Brooks. 2009. Competitive PCR reveals the complexity of post-copulatory sexual selection in *Teleogryllus commodus*. Molecular Ecology, doi:10.1111/j.1365-294X.2009.04496.x [Epub ahead of print].

Hine, E., and M. W. Blows. 2006. Determining the effective dimensionality of the genetic variance-covariance matrix. Genetics 173:1135–1144.

Hine, E., S. F. Chenoweth, and M. W. Blows. 2004. Multivariate quantitative genetics and the lek paradox: Genetic variance in male sexually selected traits of *Drosophila serrata* under field conditions. Evolution 58:2754–2762.

Hosken, D., and R. Snook. 2005. How important is sexual conflict? Am. Nat. 165:S1–S4.

Hotzy, C., and G. Arnqvist. 2009. Sperm competition favors harmful males in seed beetles. Curr. Biol. 19:404–407.

Hunt, J., M. W. Blows, F. Zajitschek, M. D. Jennions, and R. Brooks. 2007. Reconciling strong stabilizing selection with the maintenance of genetic variation in a natural population of black field crickets (*Teleogryllus commodus*). Genetics 177:875–880.

Hunt, J., C. J. Breuker, J. A. Sadowski, and A. J. Moore. 2009. Male-male competition, female mate choice and their interaction: determining total sexual selection. J. Evol. Biol. 22:13–26.

Johnson, T., and N. Barton. 2005. Theoretical models of selection and mutation on quantitative traits. Philos. Trans. R Soc. B 360:1411–1425.

Kirkpatrick, M., and M. J. Ryan. 1991. The evolution of mating preferences and the paradox of the lek. Nature 350:33–38.

Kotiaho, J. S., L. W. Simmons, and J. L. Tomkins. 2001. Towards a resolution of the lek paradox. Nature 410:684–686.

Kotiaho, J. S., N. R. Lebas, M. Puurtinen, and J. L. Tomkins. 2008. On the resolution of the lek paradox. Trends Ecol. Evol. 23:1–3.

Kruuk, L. E. B., J. Slate, J. M. Pemberton, S. Brotherstone, F. Guinness, and T. Clutton-Brock. 2002. Antler size in red deer: heritability and selection but no evolution. Evolution 56:1683–1695.

Lande, R. 1980. The genetic covariance between characters maintained by pleiotropic mutations. Genetics 94:203–216.

Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. Evolution 37:1210–1226.

Loher, W., and B. Rence. 1978. The mating behavior of *Teleogryllus commodus* (Walker) and its central and peripheral control. Z Tierpsychol. 46:225–259.

McGuigan, K., A. Van Homrigh, and M. W. Blows. 2008. An evolutionary limit to male mating success. Evolution 62:1528–1537.

Parker, G. A. 2006. Sexual conflict over mating and fertilization: an overview. Philos. Trans. R Soc. B 361:235–259.

Phillips, P. C., and S. J. Arnold. 1989. Visualizing multivariate selection. Evolution 43:1209–1222.

Pigliucci, M. 2006. Genetic variance-covariance matrices: a critique of the evolutionary quantitative genetics research program. Biol. Philos. 21:1–23.

Pischedda, A., and A. K. Chippindale. 2006. Intralocus sexual conflict diminishes the benefits of sexual selection. PLoS Biol. 4:2099–2103.

Pomiankowski, A., and A. P. Møller. 1995. A resolution of the lek paradox. Proc. R Soc. B 260:21–29.

Radwan, J. 2008. Maintenance of genetic variation in sexual ornaments: a review of the mechanisms. Genetica 134:113–127.

Reinhold, K. 2000. Maintenance of a genetic polymorphism by fluctuating selection on sex-limited traits. J. Evol. Biol. 13:1009–1014.

Robinson, M. R., J. G. Pilkington, T. H. Clutton-Brock, J. M. Pemberton, and L. E. B. Kruuk. 2008. Environmental heterogeneity generates fluctuating selection on a secondary sexual trait. Curr. Biol. 18:751–757.

Sasaki, A., and S. Ellner. 1997. Quantitative genetic variance maintained by fluctuating selection with overlapping generations: variance components and covariances. Evolution 51:682–696.

Simmons, L. W. 1986. Female choice in the field cricket *Gryllus Bimaculatus* (De Geer). Anim. Behav. 34:1463–1470.

Tomkins, J. L., J. Radwan, J. S. Kotiaho, and T. Tregenza. 2004. Genic capture and resolving the lek paradox. Trends Ecol. Evol. 19:323–328.

Tregenza, T., L. W. Simmons, N. Wedell, and M. Zuk. 2006. Female preference for male courtship song and its role as a signal of immune function and condition. Anim. Behav. 72:809–818.

Van Homrigh, A., M. Higgie, K. McGuigan, and M. W. Blows. 2007. The depletion of genetic variance by sexual selection. Curr. Biol. 17:528–532.

Wigby, S., and T. Chapman. 2005. Sex peptide causes mating costs in female Drosophila melanogaster. Curr. Biol. 15:316–321.

Zuk, M. 1987. The effects of gregarine parasites, body size, and time of day on spermatophore production and sexual selection in field crickets. Behav. Ecol. Sociobiol. 21:65–72.

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