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Evolution of genetic variation for condition-dependent traits in stalk-eyed flies

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Sexual selection has been proposed to increase genetic variation for condition-dependent ornaments. The condition capture model predicts the genetic variance for a sexually selected trait from the genetic variance in condition and the slope of the relationship between the ornament and condition. Assuming that body size reflects condition we assess the efficacy of this model using six species of stalk-eyed flies (Diopsidae). Prior evidence indicates that male eye span exhibits strong condition dependence and is under sexual selection in sexually dimorphic but not monomorphic species. In contrast, thorax width is weakly related to condition and probably under stabilizing selection. We estimated additive genetic variances for eye span, body length and thorax width from half-sib breeding studies and found that the condition capture model explained 97% of the variation in eye span genetic variance but only 7% of thorax width genetic variance. Comparison of phylogenetically independent contrasts revealed that evolutionary change in male eye span genetic variance is due to evolutionary change in the allometric relationship between eye span and condition—not to evolutionary change in genetic variance for condition. These results suggest that sexual selection can accelerate evolutionary change in condition-dependent male ornaments by increasing the genetic variation available for selection.

Keywords: Diopsidae; sexual selection; condition dependence

1. INTRODUCTION

Persistent directional selection, such as that caused by sexual selection, is often thought to deplete additive genetic variation (Falconer 1981; Charlesworth 1987). Consequently, in species where females only receive sperm from males, mate choice appears paradoxical because offspring benefit only when ornament expression and viability are heritable (Kirkpatrick & Ryan 1991; Kirkpatrick & Barton 1997). However, available evidence from diverse taxa indicates that sexually selected traits exhibit more rather than less genetic variance than traits under natural selection (Pomiankowski & Møller 1995). If generally true, this result considerably resolves the lek paradox (Borgia 1979; Taylor & Williams 1982), but demands explanation. One possibility is that modifiers which increase genetic variance will increase mean fitness whenever selection on male ornaments exhibits accelerating returns (Lande 1980; Pomiankowski & Møller 1995). This proposal has received criticism because net selection on male ornaments seems more probable to be stabilizing than directional (Rowe & Houle 1996).

Alternatively, sexually selected traits may have high levels of genetic variation when their expression depends on condition and condition exhibits genetic variation (Rowe & Houle 1996). Condition refers to the pool of resources available for allocation to the production or maintenance of traits. Consequently, an increase in the amount of resources allocated to ornament expression necessarily decreases resource availability for other traits and, therefore, imposes a cost of expression. Under this scenario, condition-dependent expression should evolve as a consequence of sexual selection because individuals with greater condition can sustain higher costs of trait exaggeration than individuals of lower condition. Genetic variation for sexually selected traits increases because these traits indicate condition. Even though condition is probably under directional selection, considerable genetic variation may be maintained by mutation because many physiological processes and, therefore, genetic loci probably influence condition (Houle 1991, 1998; Price & Schluter 1991).

Following Rowe & Houle (1996), we assume that the sexually selected trait T is a linear function of condition, i.e.

$$T = a + Cb,$$

where C is condition, a represents trait expression independent of condition and b measures the slope of the relationship between trait and condition. By assuming unlinked loci influence a, b and C and, therefore, genetic covariances involving these variables are negligible, the expectation of the genetic variance of T is approximately

$$G_T = G_a + b^2 G_c + C G_b,$$

where G_i is the genetic variance of variable i (Rowe & Houle 1996). Because sexually selected traits often exhibit condition-dependent expression (Andersson 1994), we further assume that G_a and $G_b \ll G_c$ for ornaments. In

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contrast, traits not under sexual selection should depend much less on condition and not exhibit sexual dimorphism. Consequently, the variance in naturally selected traits should be approximately G_a. Applying this model therefore requires estimation of the genetic variances for an ornament and condition as well as the degree to which the ornament scales with condition, i.e. b.

We used stalk-eyed flies (Diopsidae) to evaluate the condition capture model because some species exhibit sexual dimorphism for condition-dependent expression of eye span (David *et al*. 1998). Evidence that sexually dimorphic eye span results from sexual selection is available for *Cyrtodiopsis whitei* and *Cyrtodiopsis dalmanni*. In these two species larger eye span males are preferred for mating by females (Burkhardt & De la Motte 1988; Wilkinson & Reillo 1994; Wilkinson *et al*. 1998) and win more intrasexual contests (Panhuis & Wilkinson 1999). In contrast, neither of these effects occur in *Cyrtodiopsis quinqueguttata*, a sexually monomorphic species (Wilkinson *et al*. 1998; Panhuis & Wilkinson 1999).

We assumed that body length estimates condition. Insects with holometabolous development accumulate resources during a larval period and then allocate them to imaginal disc growth during metamorphosis (Nijhout & Emlen 1998). Once a fly has eclosed and its exoskeleton hardened, further morphological change is impossible. Therefore, the degree to which resources are allocated to eye span (b) can be estimated by the sex-specific slope of the eye span on body length regression. Genetic differences between individuals in their ability to acquire and use energy as larvae should be reflected in genetic variation for body length. Thus, for stalk-eyed flies the condition capture model predicts that the genetic variance in eye span should equal the genetic variance in body length multiplied by b^2. In contrast to eye span, thorax width in diopsids is probably under stabilizing natural selection because it determines the muscle size available for powered flight and both sexes fly to evade predators. Consequently, thorax width should be weakly related to condition and its genetic variance poorly predicted by the condition capture model. After evaluating these predictions for six species, we used a robust phylogenetic hypothesis (R. Baker, personal communication) to determine whether correlated evolution has occurred between genetic variance for condition and condition-dependent expression of eye span for each sex.

2. METHODS

(a) *Measuring condition dependence*

Because flies reared in the laboratory often exhibit little phenotypic variation in body length, we used field-collected flies to maximize the range of body lengths available and, therefore, estimated b as accurately as possible for each species. Adult *C. whitei*, *C. dalmanni*, *C. quinqueguttata* and *Teleopsis quadriguttata* were netted along streams 20–40 km north of Kuala Lumpur in peninsular Malaysia in October 1989 and January 1996. *Sphyracephala beccarri* and *Diasemopsis dubia* were netted near Pietermaritzburg, South Africa, in July 1994. Live flies were returned to Maryland and used to create stock populations. In the absence of artificial selection (Wilkinson 1993), captive rearing appears to have little effect on allometric relationships. Slopes of eye span on body length regressions for *C. whitei* collected in the field differ by 5% or less from flies reared under variable larval density from stock populations several years old (G. S. Wilkinson, unpublished data). Voucher specimens for all species are stored at the American Museum of Natural History.

For each fly we measured eye span from the outer edge of each eye bulb, body length from face to wing tip and thorax width at the widest point of the body to the nearest 0.1 mm using video-digitized images magnified $\times 56$ through a microscope. We used least squares to estimate b from both eye span and thorax width on body length regressions within each sex for each species. Due to the high correlation between these characters in all species, slope estimates derived from other regression techniques, e.g. reduced major axis, differ by less than a few per cent.

(b) *Estimating and comparing variance components*

We estimated additive genetic variance for each trait by rearing and measuring half siblings after each species had been in culture at least six generations. For each species, we reared parental generation flies under low-density conditions (David *et al*. 1998), i.e. fewer than one larva per millilitre of corn purée and housed virgins in same-sex cages for at least four weeks after eclosion to ensure sexual maturity. Two breeding methods were used. For *C. whitei* we housed each of 89 males with 15 females in vented plastic mating chambers (13 cm × 13 cm × 23 cm) and allowed these flies to mate for two weeks. Each female was subsequently isolated and allowed to lay eggs in foam-stoppered 100 ml glass jars containing 50 ml of corn purée. We then measured at least three male and three female flies from each jar that produced progeny. Because many *C. whitei* females died before laying eggs, for the remaining five species we housed each male with six females in mating chambers for two weeks and then isolated females in vented 500 ml plastic containers with 50 ml cups of food. Two male and female offspring from each dam were collected and measured. We bred the five remaining species in sequential blocks of ten sires per species. Table 1 provides the number of sires bred and progeny measured for each species.

We used restricted maximum likelihood to estimate sire variance components for each trait within each species and sex using the VARCOMP procedure in SAS v. 6.12 (SAS Institute 1997). Because we measured half-sibs, we report four times the sire variance component estimate as the additive genetic variance associated with each trait (Falconer 1981). We calculated the standard error for each genetic variance as four times the square root of the asymptotic variance of the sire variance component estimate for each trait.

We tested for differences in the magnitude of genetic variances among species using the multiple comparison Tukey–Kramer honestly significant differences (HSD) test (Neter *et al*. 1996). This procedure assumes normality of the estimates being compared. While maximum-likelihood estimates are asymptotically normal, variance component estimates are approximately χ^2 distributed and, thus, approach normality slowly as sample size increases (Searle *et al*. 1992). The natural logarithm transformation normalizes χ^2 distributed variates and can be used to normalize the sampling distribution of variance components (Box & Tiao 1973). Therefore, for each trait we tested differences in the natural log-transformed genetic variances between all pairwise combinations of species and sex using the HSD test. The standard errors used in this test were derived using the delta method (theorem 5.2 in Lehman (1983)) as $\text{s.e.}(\ln(V_a)) \approx (\text{s.e.}(V_a))/V_a$. We set the family-wide significance level for the HSD test at 0.05. Because we are assuming that the sampling

Table 1. *Means, least-squares regression slopes (b), genetic variances (G × 100), number of sires bred and progeny measured for each trait, species and sex*

(Genetic variances sharing the same letter do not differ at a family-wide level of 0.05 according to a Tukey–Kramer HSD test.)

trait and species	sex	mean ± s.e. (mm)	$b \pm$ s.e.	$G \pm$ s.e.	progeny (sires)
eye span					
C. whitei	male	8.23 ± 0.07	2.23 ± 0.06	28.29 ± 18.9a	1387 (42)
	female	5.85 ± 0.03	1.12 ± 0.02	9.49 ± 3.79ab	2738 (59)
C. dalmanni	male	9.34 ± 0.04	2.33 ± 0.06	25.83 ± 8.00a	609 (90)
	female	6.31 ± 0.02	1.14 ± 0.03	7.22 ± 2.99abc	638 (91)
D. dubia	male	7.26 ± 0.03	1.05 ± 0.11	5.81 ± 3.36abc	387 (63)
	female	5.32 ± 0.03	0.76 ± 0.05	8.75 ± 3.97abc	353 (63)
T. quadriguttata	male	3.93 ± 0.01	0.71 ± 0.03	1.32 ± 0.91bcd	339 (63)
	female	3.99 ± 0.01	0.63 ± 0.04	0.98 ± 0.39cd	350 (64)
C. quinqueguttata	male	4.58 ± 0.01	0.69 ± 0.03	0.61 ± 0.34cd	591 (82)
	female	4.64 ± 0.01	0.67 ± 0.04	0.62 ± 0.33cd	603 (82)
S. beccarri	male	2.13 ± 0.01	0.54 ± 0.04	0.55 ± 0.15cd	772 (92)
	female	2.17 ± 0.01	0.35 ± 0.03	0.50 ± 0.13d	718 (90)
thorax width					
C. whitei	male	1.66 ± 0.01	0.26 ± 0.01	0.62 ± 0.34ab	1387 (42)
	female	1.70 ± 0.01	0.28 ± 0.01	0.84 ± 0.31ab	2738 (59)
C. dalmanni	male	1.97 ± 0.01	0.29 ± 0.01	0.92 ± 0.26ab	609 (90)
	female	1.94 ± 0.01	0.30 ± 0.01	1.44 ± 0.32a	638 (91)
D. dubia	male	1.83 ± 0.04	0.23 ± 0.03	0.69 ± 0.65ab	387 (63)
	female	1.91 ± 0.05	0.29 ± 0.03	0.28 ± 0.21ab	353 (63)
T. quadriguttata	male	1.71 ± 0.01	0.27 ± 0.03	1.66 ± 0.72ab	339 (63)
	female	1.79 ± 0.01	0.21 ± 0.07	0.34 ± 0.16ab	350 (64)
C. quinqueguttata	male	2.03 ± 0.01	0.31 ± 0.02	0.20 ± 0.11b	591 (82)
	female	2.14 ± 0.01	0.32 ± 0.02	0.38 ± 0.14ab	603 (82)
S. beccarri	male	1.40 ± 0.01	0.37 ± 0.04	0.83 ± 0.17ab	772 (92)
	female	1.57 ± 0.01	0.24 ± 0.05	1.29 ± 0.26ab	718 (90)
body length					
C. whitei	male	6.65 ± 0.03	—	6.16 ± 3.78ab	1387 (42)
	female	6.72 ± 0.02	—	4.75 ± 2.41abc	2738 (59)
C. dalmanni	male	7.45 ± 0.02	—	5.09 ± 1.48ab	609 (90)
	female	7.14 ± 0.02	—	6.82 ± 1.56a	638 (91
D. dubia	male	6.59 ± 0.01	—	1.65 ± 1.00abc	387 (63)
	female	6.70 ± 0.02	—	1.98 ± 3.27abc	353 (63)
T. quadriguttata	male	5.87 ± 0.02	—	5.99 ± 2.29ab	341 (63)
	female	6.12 ± 0.02	—	4.59 ± 1.50abc	351 (64)
C. quinqueguttata	male	7.39 ± 0.01	—	3.27 ± 1.04abc	591 (82)
	female	7.66 ± 0.02	—	4.71 ± 1.29ab	603 (82)
S. beccarri	male	4.52 ± 0.01	—	1.07 ± 0.36c	772 (92)
	female	4.98 ± 0.01	—	1.20 ± 0.40bc	718 (90)

distribution of $\ln(V_a)$ is Gaussian, infinite degrees of freedom are used for the HSD comparisons.

(c) *Comparative analyses*

To determine whether evolutionary change in genetic variation for eye span was caused by evolutionary change in body length or in condition-dependent expression we used phylogenetically independent contrasts (Felsenstein 1985). We assumed a gradual model of evolution by standardizing contrasts with branch lengths (Garland *et al*. 1992; Purvis & Rimbaut 1994) obtained from a molecular phylogenetic analysis of 33 diopsid species and two outgroup taxa (R. Baker, personal communication). To assess the significance of relationships between variables we fitted least squares regressions through the origin (Harvey & Pagel 1991).

3. RESULTS

Inspection of table 1 reveals that three species are sexually dimorphic for eye span while three are sexually monomorphic. Male relative eye span (eye span/body length) exceeds female relative eye span in *C. whitei* (1.24 for males and 0.87 for females), *C. dalmanni* (1.25 for males and 0.88 for females) and *D. dubia* (1.10 for males and 0.79 for females), but does not differ between the sexes in *C. quinqueguttata* (0.62 for males and 0.61 for females), *T. quadriguttata* (0.67 for males and 0.65 for females) and *S. beccarrii* (0.47 for males and 0.44 for females). Eye span condition dependence also differs between species and sexes (figure 1). Analysis of covariance (ANCOVA) on eye span revealed significant main effects of species ($F_{5,830} = 82.0$ and $p < 0.0001$), sex ($F_{1,830} = 424.5$ and $p < 0.0001$) and body length ($F_{1,830} = 1596.6$ and $p < 0.0001$) as well as significant interactions between species and body length ($F_{1,830} = 199.2$ and $p < 0.0001$), sex and body length ($F_{1,830} = 648.1$ and $p < 0.0001$) and the three-way term ($F_{1,830} = 519.3$ and $p < 0.0001$). Comparison of eye span on body length regression slopes between the sexes for each of the six species indicated that *C. whitei*, *C. dalmanni*,

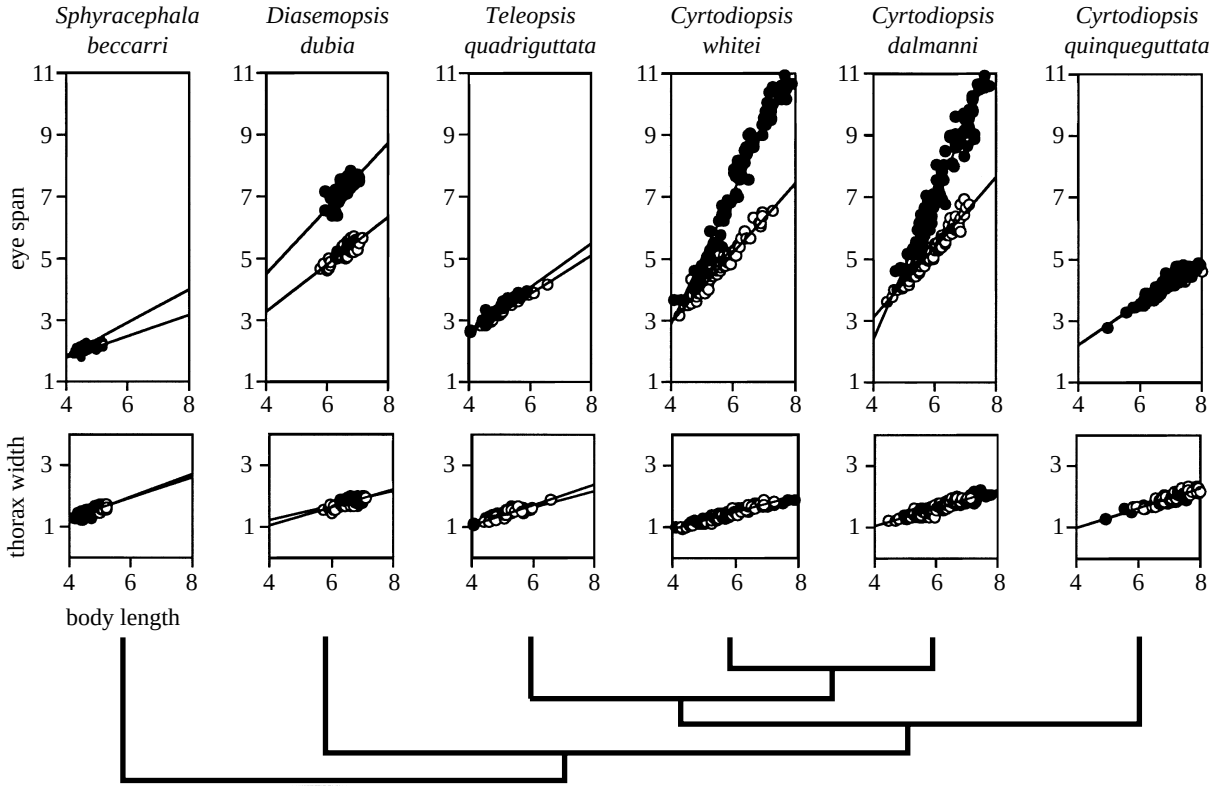

Figure 1. Bivariate plots of eye span and thorax width against body length for field-collected specimens of six species of stalk-eyed flies. Males are represented by filled circles and females by open circles. Lines represent least-squares regressions for each sex. The phylogenetic relationships between the species are indicated beneath the plots.

D. dubia and *S. beccarri* differ between the sexes in condition dependence, while *C. quinqueguttata* and *T. quadriguttata* do not. *C. quinqueguttata* and *T. quadriguttata* showed no difference in eye span–body length slope (Bonferroni-adjusted $p = 0.003$).

Thorax width also covaried with body length in all species (ANCOVA $F_{1,830} = 1372.2$ and $p < 0.0001$) but did so weakly relative to eye span (figure 1). The regression slopes for thorax width on body length were one-quarter to one-eighth of those for eye span on body length in the three eye span dimorphic species (table 1). Condition-dependent expression of thorax width was not sexually dimorphic ($F_{1,830} = 1.91$ and $p = 0.17$) and did not differ between species ($F_{5,830} = 0.99$ and $p = 0.42$). Only one interaction term in the ANCOVA, that between species and body length ($F_{5,830} = 3.27$ and $p = 0.006$), was significant. Examination of all 15 possible species-pair ANCOVAs revealed that the thorax width–body length slope for *S. beccarri* differed (Bonferroni-adjusted $p < 0.003$) from all other species except *C. quinqueguttata*. In addition, slopes differed between *C. quinqueguttata* and *C. whitei*. Taken together, these results indicate that condition-dependent expression of eye span has evolved independently from condition-dependent expression of flight muscles.

Estimates of the genetic variances for eye span, body length and thorax width are given in table 1 for each sex and species. The Tukey HSD test revealed that only one out of 60 pairwise comparisons of genetic variances for thorax width was significant. Furthermore, only five out of 60 comparisons of body length genetic variances differed and all involved *S. beccarrii*, the species with the smallest body size. In contrast, 27 out of 60 pairwise comparisons of eye span genetic variances exhibited significance and involved the three species with elongated eye span, *C. whitei*, *C. dalmanni* and *D. dubia*, paired with the three monomorphic species, *S. beccarrii*, *C. quinqueguttata* and *T. quadriguttata*.

The condition capture model predicts the magnitude of genetic variance in eye span for both sexes of all six species with remarkable accuracy (figure 2*a*). The predicted genetic variances explain 97% of the observed variation. In contrast, the model does poorly at predicting genetic variance for thorax width and only explains 7% of the observed variation (figure 2*b*).

The significance of the fit in figure 2 is unclear because each sex and species are not phylogenetically independent. Therefore, to determine whether the condition capture model predicts evolutionary change in genetic variances we compared independent contrasts for genetic variance in eye span against the contrasts in condition capture predictions for each sex separately (figure 3). Regression through the origin revealed that changes in genetic variation for eye span significantly correlated with changes in the condition capture prediction estimates for males (figure 3*a*, $r^2 = 0.95$ and $p < 0.001$) but not females (figure 3*b*, $r^2 = 0.55$ and $p = 0.09$). The relationship in figure 3*a* could be due to correlated change in condition-dependent expression, i.e. b^2 or in condition variance, i.e. G_{bl}. Independent contrast comparisons supported the former possibility. Change in eye span genetic variance correlated with change in the squared slope between eye span and body length for both males (figure 3*c*, $r^2 = 0.95$ and $p < 0.001$) and females (figure 3*d*, $r^2 = 0.89$ and $p = 0.005$). In contrast, genetic variation for body length

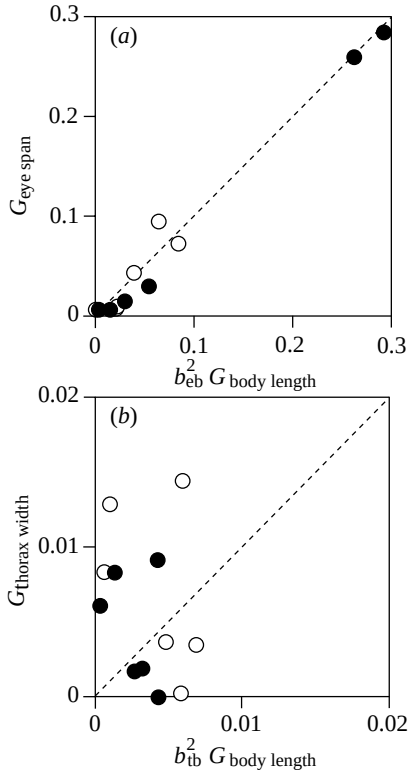

Figure 2. Genetic variance estimates for (*a*) eye span and (*b*) thorax width plotted against the condition capture predictions based on genetic variance in body length multiplied by the squared phenotypic regression slope for each trait on body length. Males are indicated by filled circles and females by open circles.

does not exhibit correlated evolution with genetic variation for eye span in either males ($r^2 = 0.02$ and $p = 0.83$) or females ($r^2 = 0.09$ and $p = 0.62$). Thus, evolutionary change in genetic variation for a trait under sexual selection in males has been accompanied by evolutionary change in the form of the relationship between the trait and condition, not in condition itself.

4. DISCUSSION

Despite evidence for intense sexual selection in extant populations of stalk-eyed flies (Wilkinson & Reillo 1994; Wilkinson *et al*. 1998), we found over 20 times as much genetic variation for male eye span in two species (*C. whitei* and *C. dalmanni*) with the most extreme sexual dimorphism, than in two sexually monomorphic related species (*C. quinqueguttata* and *T. quadriguttata*). Similarly, *D. dubia* exhibited approximately ten times the genetic variation in eye span as *S. beccarri*. Given the putative phylogenetic relationships between these species (cf. figure 1), increased genetic variation for eye span appears to be derived and associated with eye span sexual dimorphism. Using a simple linear model, we accurately predicted evolutionary change in genetic variation for eye span but not for thorax width, as expected if eye span is under sexual selection and thorax width is under stabilizing natural selection. Variation in thorax width is consistent with stabilizing selection, i.e. this trait shows weak condition dependence, absence of sexual dimorphism and little variation between species. Regression analyses using phylogenetically independent contrasts indicated that evolutionary change in genetic variation for eye span is due to change in condition dependence rather than change in genetic variation for condition. Thus, all of our results are consistent with capture of genetic variation in condition by sexually selected traits.

Nevertheless, we cannot reject the alternative model proposed by Pomiankowski & Møller (1995). The differences in eye span condition dependence among diopsid species must depend on genetic factors that modify how eye span grows relative to other body parts. Pomiankowski & Møller (1995) explicitly proposed that genetic modifiers would influence condition-dependent expression of sexual traits and lead to an increase in genetic variation. They further proposed that selection on eye span should be concave upwards such that increasing ornament variance will lead to increased mean fitness (Lande 1980). Because large eye span males are both attractive to females (Wilkinson *et al*. 1998) and able to defend nocturnal mating aggregations, selection gradients estimated on adult flies are concave upwards (Wilkinson & Reillo 1994; G. S. Wilkinson, unpublished data), as predicted. While correlated selection may operate against genes for increasing eye span at some other life-history stage, such as during metamorphosis, net directional selection for longer eye span must have occurred in the past to account for the recurrent evolution of eye span sexual dimorphism in the family (Wilkinson & Dodson 1997).

In applying the condition capture model to stalk-eyed flies we assumed that adult body size reflects condition in holometabolous insects. This assumption is consistent with experimental work, which has shown that manipulating larval density alters eye span more than body size in male *C. dalmanni* (David *et al*. 1998). Thoracic horn size in male dung beetles shows similar sensitivity to diet manipulation, which affects body size (Emlen 1997). Our ability to predict change in genetic variance for eye span but not thorax width also provides support for this assumption. If adult body size was independent of condition, then the model should not have predicted genetic variances for either trait. This assumption may not be justified, however, when resource acquisition can influence production of a sexually selected trait independently of body size, such as may occur in organisms with indeterminate growth or behavioural displays.

These results have several significant implications for understanding how sexually selected traits evolve. First, in contrast to traits under natural selection (Arnold 1992), genetic variances in sexually selected traits are unlikely to be stationary over time. Thus, evolutionary change in means cannot be predicted reliably by assuming constant genetic variances. Second, because variances tend to increase in response to directional selection on a trait, evolutionary rates for sexually selected characters should increase, all else being equal. Therefore, condition capture could lead to accelerated evolutionary change in ornament expression between populations experiencing different selection pressures. To the extent that condition-dependent ornaments affect mate selection, such changes could influence speciation (Lande 1981). Third, changes in genetic variances will almost certainly co-occur with

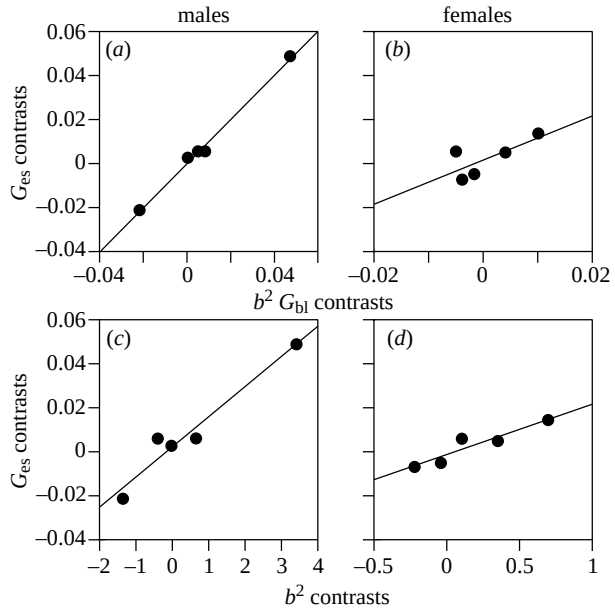

Figure 3. Standardized independent contrasts for genetic variation in eye span plotted against standardized independent contrasts for the condition capture predictions for (*a*) males and (*b*) females. The degree to which change in genetic variation for eye span correlates with change in condition-dependent slopes is indicated for (*c*) males and (*d*) females.

changes in genetic covariances between characters. In particular, genetic covariances involving condition will probably change. To the extent this is true, prediction of multivariate response to selection, for example (Lande & Arnold 1983), will be in error. Further study is needed to determine the magnitude of change in genetic covariances which do or do not involve condition-dependent traits.

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REFERENCES

Andersson, M. 1994 *Sexual selection*. Princeton University Press.

Arnold, S. J. 1992 Constraints on phenotypic evolution. *Am. Nat.* **140**, S85–S107.

Borgia, G. 1979 Sexual selection and the evolution of mating systems. In *Sexual selection and reproductive competition in insects* (ed. M. S. Blum & N. A. Blum), pp. 19–80. New York: Academic Press.

Box, G. E. P. & Tiao, G. C. 1973 *Bayesian inference in statistical analysis*. Reading, MA: Addison-Wesley Publishing Co.

Burkhardt, D. & De la Motte, I. 1988 Big 'antlers' are favoured: female choice in stalk-eyed flies (Diptera, Insecta), field collected harems and laboratory experiments. *J. Comp. Physiol.* A **162**, 649–652.

Charlesworth, B. 1987 The heritability of fitness. In *Sexual selection: testing the alternatives* (ed. J. W. Bradbury & M. B. Andersson), pp. 21–40. Chichester, UK: Wiley.

David, P., Hingle, A., Greig, D., Rutherford, A., Pomiankowski, A. & Fowler, K. 1998 Male sexual ornament size but not asymmetry reflects condition in stalk-eyed flies. *Proc. R. Soc. Lond.* B **265**, 2211–2216.

Emlen, D. J. 1997 Diet alters male horn allometry in the beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). *Proc. R. Soc. Lond.* B **264**, 567–594.

Falconer, D. S. 1981 *Introduction to quantitative genetics*. New York: Longman.

Felsenstein, J. 1985 Phylogenies and the comparative method. *Am. Nat.* **126**, 1–25.

Garland, T., Harvey, P. H. & Ives, A. R. 1992 Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Syst. Biol.* **41**, 18–42.

Harvey, P. H. & Pagel, M. D. 1991 *The comparative method in evolutionary biology*. Oxford University Press.

Houle, D. 1991 Genetic covariance of fitness correlates: what genetic correlations are made of and why it matters. *Evolution* **45**, 630–649.

Houle, D. 1998 How should we explain variation in the genetic variance of traits? *Genetica* **102/103**, 241–253.

Kirkpatrick, M. & Barton, N. H. 1997 The strength of indirect selection on female mating preferences. *Proc. Natl Acad. Sci. USA* **94**, 1282–1286.

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

Lande, R. 1980 Genetic variation and phenotypic evolution during allopatric speciation. *Am. Nat.* **116**, 463–479.

Lande, R. 1981 Models of speciation by sexual selection on polygenic traits. *Proc. Natl Acad. Sci. USA* **78**, 3721–3725.

Lande, R. & Arnold, S. J. 1983 The measurement of selection on correlated characters. *Evolution* **36**, 1210–1226.

Lehman, E. L. 1983 *Theory of point estimation*. New York: Wiley.

Neter, J., Kutner, M. H., Nachtsheim, C. J. & Wasserman, W. 1996 *Applied linear statistical models*. Chicago, IL: Richard D. Irwin, Inc.

Nijhout, F. & Emlen, D. 1998 Competition among body parts in the development and evolution of insect morphology. *Proc. Natl Acad. Sci. USA* **95**, 3685–3689.

Panhuis, T. M. & Wilkinson, G. S. 1999 Exaggerated male eye span influences contest outcome in stalk-eyed flies. *Behav. Ecol. Sociobiol.* **46**. (In the press.)

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

Price, T. & Schluter, D. 1991 On the low heritability of life-history traits. *Evolution* **45**, 853–862.

Purvis, A. & Rimbaut, A. 1994 *Comparative analysis by independent contrasts (CAIC), version 2*. Oxford University Press.

Rowe, L. & Houle, D. 1996 The lek paradox and the capture of genetic variance by condition-dependent traits. *Proc. R. Soc. Lond.* B **263**, 1415–1421.

SAS Institute 1997 *SAS, v. 6.12*. Cary, NC: SAS Institute.

Searle, S. R., Casella, G. & McCulloch, C. E. 1992 *Variance components*. New York: Wiley.

Taylor, P. D. & Williams, G. C. 1982 The lek paradox is not resolved. *Theor. Popul. Biol.* **22**, 392–409.

Wilkinson, G. S. 1993 Artificial selection alters allometry on the stalk-eyed fly *Cyrtodiopsis dalmanni* (Diptera: Diopsidae). *Genet. Res.* **62**, 213–222.

Wilkinson, G. S. & Dodson, G. 1997 Function and evolution of antlers and eye stalks in flies. In *The evolution of mating systems in insects and arachnids* (ed. J. Choe & B. Crespi), pp. 310–328. Cambridge University Press.

Wilkinson, G. S. & Reillo, P. R. 1994 Female preference response to artificial selection on an exaggerated male trait in a stalk-eyed fly. *Proc. R. Soc. Lond.* B **255**, 1–6.

Wilkinson, G. S., Kahler, H. & Baker, R. H. 1998 Evolution of female mating preferences in stalk-eyed flies. *Behav. Ecol.* **9**, 525–533.