Artificial sexual selection alters allometry in the stalk-eyed fly *Cyrtodiopsis dalmanni* (Diptera: Diopsidae)

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Summary

Selection for increased and decreased ratio of eye span to body length was exerted on male stalk-eyed flies (*Cyrtodiopsis dalmanni*) from Malaysia using replicate selected and unselected lines. Response to selection was symmetrical. After 10 generations high line male eye span increased to 1·3 body lengths while low line male eye span declined to 1·1 body lengths. Realized heritabilities for eye span to body length ratio, estimated using regressions of deviations from unselected controls on cumulative selection differentials, were greater than zero for all four selected lines with average $h^2 = 0·35 \pm 0·06$. The static linear allometric relationship between eye span and body length diverged between selected lines and rotated among selected line males in the same direction as among males in other sexually dimorphic diopsid species. Crosses between lines after 13 generations of selection indicate that the genes which influence relative eye span combine additively and do not exhibit sex linkage or maternal effects. The genetic correlation between the sexes, $0·29 \pm 0·05$ as estimated by the regression of female on male change in eye span, did not prevent sexual dimorphism in eye span from diverging between lines. These results suggest that the exaggerated eye span of male *C. dalmanni* is maintained by natural selection opposing sexual selection rather than by lack of or asymmetry in additive genetic variation. Furthermore, the variation in sexual dimorphism for eye span–body length allometry observed among extant diopsid species is consistent with sexual selection of variable intensity acting on relative eye span.

1. Introduction

Exaggerated sex-limited weapons or ornaments favored by sexual selection may attain a limit for one of two reasons. Either additive genetic variation for continued elaboration is exhausted or natural selection opposes further exaggeration and results in stabilizing selection where additive genetic variation is maintained by a balance between mutation and selection (Fisher, 1958; Lande, 1976; Lande, 1981). Either persistent female choice of a male character or elaboration of a structure used to settle male contests could lead to either genetic outcome (Lande, 1981; Charlesworth, 1984; Maynard Smith & Brown, 1986).

Although field estimates of heritability (Prout & Barker, 1989; Riska *et al.* 1989) have not been reported, breeding experiments on a variety of insects (Carson & Lande, 1984; Butlin & Hewitt, 1986; McLain, 1987; Simmons, 1987; Wilkinson, 1987; Hedrick, 1988; Moore, 1989; Simmons & Ward, 1991) and fish (Houde, 1992; Bakker, 1993) indicate that sexually-selected characters typically possess

additive genetic variation. Thus, continued elaboration of sexually-selected traits, at least in these species, is not prohibited by lack of genetic variation. However, breeding experiments do not reveal if response to selection will be symmetrical.

If sexually dimorphic traits have experienced prolonged directional selection, then less additive genetic variation for increased than for decreased elaboration can be expected for at least three reasons. Mutations may reduce the expression of a complex sexually-selected trait more often than increase it (Pomiankowski *et al.* 1991), the frequencies of genes that influence the trait may be near their upper limits (Falconer, 1981), and genes that influence the trait may exhibit directional dominance (Fisher, 1958). Artificial selection on a male display or combat character should, therefore, result in more rapid evolutionary response toward reduced expression than toward increased elaboration. Unfortunately, symmetry of response cannot be evaluated in the two studies (Cade, 1981; Carson & Teramoto, 1984) where artificial selection was exerted on sexually-

selected traits because selection only proceeded for a few generations and the response was not measured as a deviation from controls. However, 24 of 30 attempts to select divergently on a reproductive fitness trait have shown higher realized heritabilities for diminished than improved performance (Frankham, 1990), as expected if breeding values are not normally distributed around phenotypic means.

In this study I exerted divergent selection on an exaggerated male trait to assess symmetry of response and the extent to which genes influencing that trait act additively. The study organism is the Malaysian stalk-eyed fly, *Cyrtodiopsis dalmanni*, and the trait is relative male eye span, i.e. the ratio of the distance between the tips of a male's eyes and his body length (Fig. 1). Sexual dimorphism in eye span is pronounced in this and the sympatric congener, *C. whitei*, because the slope of the regression of eye span on body length, or what I will refer to as linear static allometry (Cock, 1966; Klingenberg & Zimmermann, 1992), is greater than one in males but less than one in females (Shillito, 1971; Burkhardt & de la Motte, 1985). Consequently, differences in eye span magnify differences in body size in males.

The static allometric relationship between eye span and body length also varies greatly between males of different diopsid species (Burkhardt & de la Motte, 1985). For example, *C. quinqueguttata* and the more primitive *Sphyrecephala brevicornis* (Feijen, 1989) exhibit no dimorphism in eye span and no difference between the sexes in eye span–body length allometry (Burkhardt & de la Motte, 1985; unpublished data). Because the eye span on body length regression for *C. quinqueguttata* is similar in slope to that of female *C. whitei* and *C. dalmanni* (Burkhardt & de la Motte, 1985), the elevated slope of male *C. whitei* and *C. dalmanni* eye span on body length regressions probably represents an evolutionarily derived state. Furthermore, elongated eye spans among male *C. whitei* and *C. dalmanni* do not represent a correlated response to selection for larger size (Lande, 1979) because males of these species are typically smaller in length than male *C. quinqueguttata* (Burkhardt & de la Motte, 1985). Similar increases in the slope of male eye span–body length regressions have occurred between sexually monomorphic and dimorphic species in at least three other genera of diopsids (Burkhardt & de la Motte, 1985; unpublished data). Thus, in addition to determining eye span response to selection, I also examine male and female allometric relationships for any correlated responses to selection. A response in eye span–body length allometry to sexual selection on relative eye span would demonstrate additive genetic variation for static allometry and provide a mechanism for the diversification of male morphology observed in this group of unusual flies.

Available evidence indicates that sexual selection could influence sexual dimorphism for eye span in *C. dalmanni* and *C. whitei*. Every evening flies of these species gather into aggregations on root threads under overhanging embankments along forest streams in Malaysia. Males compete for control of groups of females by comparing eye spans and escalate confrontations by grappling with their forelegs when eye span is similar (de la Motte & Burkhardt, 1983). Winners of contests invariably displace smaller males prior to darkness and at dawn mate with most of the females in the aggregation (Lorch *et al.* 1993). *C. whitei* females prefer to alight near model males with experimentally elongated eye span (Burkhardt & de la Motte, 1988) suggesting that female choice, in addition to male competition, may favor exaggerated eye span in these flies.

2. Materials and methods

(i) *Laboratory procedures*

Over 200 *C. dalmanni* were netted along small forest streams near Kuala Lumpur, Malaysia, transported to Maryland, and housed in a $40 \times 40 \times 120$ cm population cage in January 1989. This cage is kept in a 25 °C constant temperature room on a 12 h light–dark cycle with a 30 min dawn/dusk period provided by a 25 W incandescent light. Humidity is kept high by lining the cage with moist cotton and blotting paper. Twice each week fresh ears of corn are ground and provided in disposable dishes as food for adults. Mold is inhibited by adding 5 ml of a 10 % solution of methylparaben in 90 % ethanol to each liter of corn pulp prior to autoclaving for 30 min. Because flies both feed and oviposit on the processed corn, larvae are reared by introducing food in plastic cups rather than dishes. Twice each week these food cups are transferred into larger 500 ml containers lined with damp cotton and plugged with foam stoppers to permit the larvae to climb out of the cups and pupate in the cotton. Newly eclosed flies are returned to the cage as necessary to maintain the population at approximately 300 flies. Because the minimum generation time is eight weeks and adult flies live six months or more in captivity (unpublished data), the base population had been in captivity for less than 7 generations prior to the onset of selection in March 1991.

Artificial sexual selection was exerted on the ratio of eye span to body length in males for four replicate lines. Two lines each were selected for high and low ratios by taking either the 10 highest or 10 lowest ratios of 50 measured males and housing them with 25 randomly selected virgin females in a $40 \times 40 \times 40$ cm cage. Two unselected lines were maintained at the same time by randomly selecting 10 males and 25 females. Larvae were reared in incubators at 25 ± 1 °C in cups containing 50 ml of corn pulp. Any pupae remaining in cups were transferred to the cotton before eclosion. Three cups of food were provided twice each week for two weeks to obtain flies for the
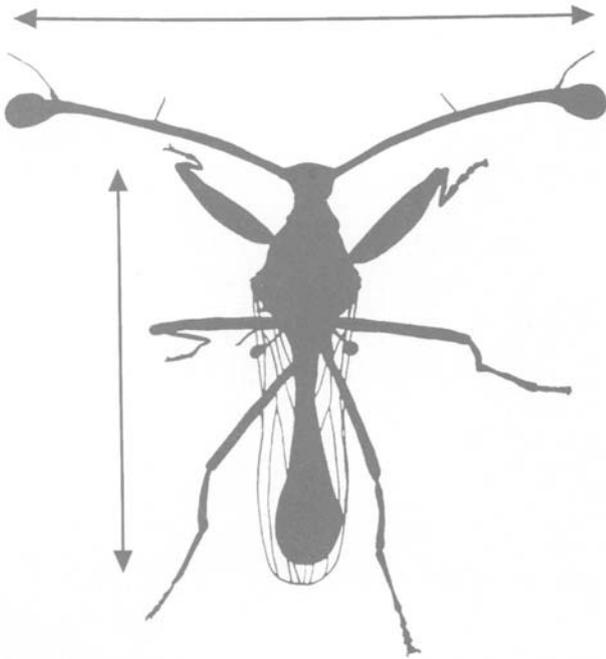
Fig. 1. Silhouette of the stalk-eyed fly, *Cyrtodiopsis dalmanni*, with arrows indicating how eye span and body length are measured.

first 8 generations. Beginning in generation nine we provided 4 cups at each feeding to minimize larval crowding. Under these conditions and after nine generations of selection each female produced an average of 2·5 pupae per day with no differences in pupal production detectable between the six lines.

Using CO_2 anesthesia, assistants and I measured flies resting on their orbital and thoracic spines from a ×56 video image digitized into a Macintosh computer, which provides a resolution of 50 pixels/mm. Using the program Image 1.31 we measured eye span from the outer edges of the ommatidia, body length from face to wing tip, and thorax width at the widest point on each animal (Fig. 1). Thorax width was included to determine if eye span correlated with body width. The ratio of eye span to body length will hereafter be referred to as relative eye span.

(ii) *Analysis*

Assuming that genetic variation has not changed during selection, an unbiased estimator of the heritability, h^2, is the regression coefficient, b, from a least squares regression of response on cumulative selection differential (Hill, 1972a). To control for environmental variation between generations, I measured response as the deviation in the mean of each trait in a selected line from the mean in the corresponding control line and fitted the regressions without a constant. The standard sampling variance of a regression coefficient underestimates the true sampling variance of a regression on cumulative selection because it only

considers measurement error variance, not drift variance. While measurement error is independent of generation, drift variance accumulates over generations (Hill, 1971). When response is measured as a deviation from a control line, the expected measurement error variance, σ_e^2, and drift variance, σ_d^2, are

$$\sigma_e^2 = (1 - h^2)\,\sigma^2/M_e + \sigma^2/M_e$$

and

$$\sigma_d^2 = h^2(1 - h^2)\,\sigma^2/N_e + \sigma^2 h^2/N_e,$$

where σ^2 is the phenotypic variance, N_e is the effective number of individuals selected or mated and M_e is the effective number measured each generation (Hill, 1972b). I estimated N_e and M_e as

$$\frac{1}{N_e} = \frac{1}{4N_m} + \frac{1}{4N_f}$$

$$\frac{1}{M_e} = \frac{1}{4M_m} + \frac{1}{4M_f}$$

(Hill, 1972a). Given the selection regime described above, $N_e = 28\cdot6$ and $M_e = 66\cdot7$. I estimated σ^2 as the within-generation mean squares from a one-way ANOVA with generation as the grouping factor. By assuming that the selection differential is constant each generation, i.e. the average selection differential, $\bar{S}$, is $\Sigma S/2t$ where ΣS is the cumulative selection differential on males, and t is the number of generations, the expected sampling variance for b is

$$V_b = \frac{6}{\sigma^2 t(t+1)(2t+1)}\left(\frac{2t^2 + 2t + 1}{5}\sigma_d^2 + \sigma_e^2\right)$$

(Hill, 1972a). The standard error of b, therefore, is $\sqrt{V_b}$.

All statistical tests use two-tailed probabilities and were computed using SYSTAT 5.1 for the Macintosh (Wilkinson, 1989).

3. Results

(i) *Responses to selection*

Significant changes to relative and absolute eye span, body length and thorax width in both males and females were detected after 10 generations of selection (Tables 1 and 2). Thus, artificial sexual selection caused a direct response in relative eye span of males and correlated responses in other traits including the relative eye span of females. The magnitude of the F-ratios and the squared correlation coefficients for selection treatment indicate that much greater changes occurred between lines for relative and absolute eye span than for body length or thorax width (Table 2). Because eye span and body length are sexually dimorphic in *C. dalmanni*, sex also accounted for a

Table 1. *Trait means* (s.e.) *in mm after 10 generations of selection. Sample size equals 50 for each replicate with the exception of L2 males for which there were 34*

Sex	Line	Eye span/ body length	Eye span	Body length	Thorax width
Male	H1	1·277 (0·005)[a]	9·19 (0·06)[a]	7·19 (0·03)[a]	1·98 (0·01)[a]
	H2	1·299 (0·005)[b]	9·16 (0·05)[a]	7·05 (0·03)[b]	1·96 (0·01)[a]
	U1	1·217 (0·005)[c]	8·48 (0·07)[b]	6·97 (0·04)[b]	1·90 (0·01)[b]
	U2	1·234 (0·004)[c]	8·66 (0·04)[b]	7·02 (0·02)[b]	1·93 (0·01)[b]
	L1	1·157 (0·005)[d]	7·97 (0·05)[c]	6·89 (0·03)[b]	1·91 (0·01)[b]
	L2	1·115 (0·005)[e]	7·83 (0·07)[c]	7·02 (0·04)[b]	1·90 (0·01)[b]
Female	H1	0·905 (0·003)[f]	6·24 (0·03)[d]	6·90 (0·03)[c]	1·93 (0·01)[b]
	H2	0·896 (0·004)[f]	6·03 (0·03)[de]	6·73 (0·04)[c]	1·88 (0·01)[b]
	U1	0·865 (0·003)[g]	5·86 (0·04)[e]	6·78 (0·04)[c]	1·89 (0·01)[b]
	U2	0·869 (0·003)[g]	5·96 (0·03)[e]	6·86 (0·03)[c]	1·89 (0·01)[b]
	L1	0·824 (0·003)[h]	5·56 (0·03)[f]	6·74 (0·03)[c]	1·91 (0·01)[b]
	L2	0·816 (0·003)[h]	5·59 (0·03)[f]	6·85 (0·03)[c]	1·92 (0·01)[b]

[a-h] Indicate lack of significant differences between means with identical superscripts in each column according to Tukey HSD posthoc tests.

Table 2. *F-ratios and squared correlation coefficients from nested ANOVAs on each of the four traits measured after 10 generations of selection. Total sample size is 584 flies*

Source	D.F.	Eye span/ body length	Eye span	Body length	Thorax width
Treatment	2	790·7**	391·6**	8·3**	15·4**
Sex	1	22737·5**	10342·6**	132·8**	29·2**
Replicate within treatment	1	13·2**	6·2**	14·3**	2·6
Treatment × sex	2	74·6**	58·4**	6·3**	13·8**
R^2		0·98	0·95	0·27	0·15

* Significant at 1%; ** significant at 0·1%.

significant fraction of the variation in each trait (Table 2). For each trait the correlated response in females was less than the response in males; therefore, a significant sex-by-treatment interaction was present for all traits. Significant differences were also detected between replicates within selection regimes for relative eye span, absolute eye span and body length but not thorax width (Table 2). Post hoc tests indicate that the two low line replicates differed, but not the two high line replicates, for these traits (Table 1). Even though body length differs between the sexes in unselected flies, body length only changed in one of the high lines for males and did not change across lines within females (Table 1). Thorax width increased in high line males, but otherwise showed no differences between lines or sexes (Table 1).

The bidirectional response to selection demonstrates that additive genetic variation is present for relative and absolute eye span (Fig. 2). The regression of the cumulative response, as measured by the difference between the selected and control lines, on the cumulative selection differential for relative eye span revealed heritabilities significantly greater than zero for all four selected lines (Table 3). The estimated

Table 3. *Phenotypic variance, σ^2, mean selection differential, $\bar{S}$, mean selection intensity, i, and heritability, h^2, for eye span/body length among males in each selected line. The heritability is the slope of a regression with zero intercept of cumulative response on half the cumulative selection differential*

Line	σ^2	$\bar{S}$	i	$h^2 \pm$ s.e.
H1	0·001 19	0·023	0·67	0·35 ± 0·05
H2	0·001 27	0·025	0·70	0·35 ± 0·05
L1	0·001 18	0·021	0·61	0·22 ± 0·04
L2	0·001 41	0·025	0·67	0·49 ± 0·05
Mean	0·001 26	0·024	0·66	0·35 ± 0·06

standard errors on the heritabilities within each selected line were comparable to the standard error calculated directly from the four selected lines (Table 3). Thus, the apparent differences in heritability between replicates are consistent with sampling error and drift.

Males and females in the two unselected replicates decreased in eye span (Fig. 2) and body length over
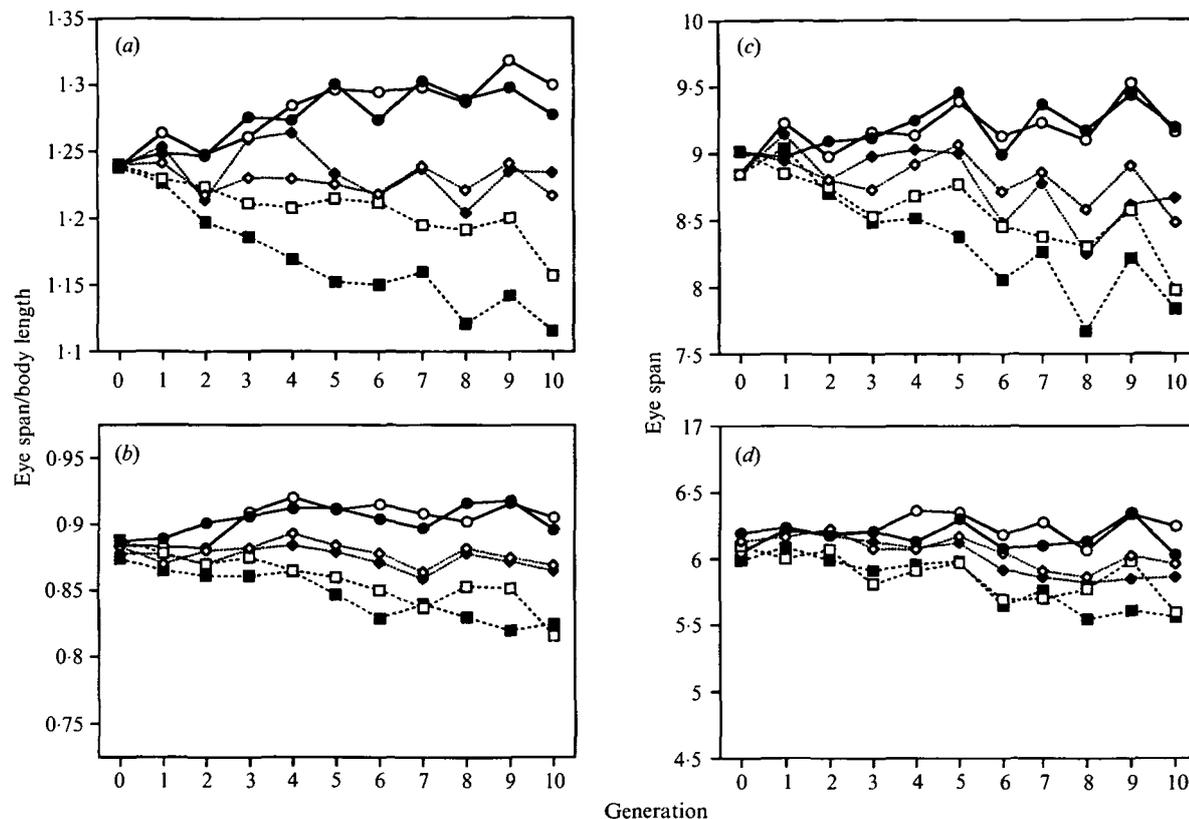
Fig. 2. Response to selection on male eye span to body length ratio plotted against generation number for relative eye span in (a) males and (b) females and eye span (mm) in (c) males and (d) females. Circles represent lines selected for increased male eye span to body length ratio, squares correspond to lines selected for decreased male relative eye span, and diamonds indicate unselected control lines. Matched replicates are indicated by symbol fill.
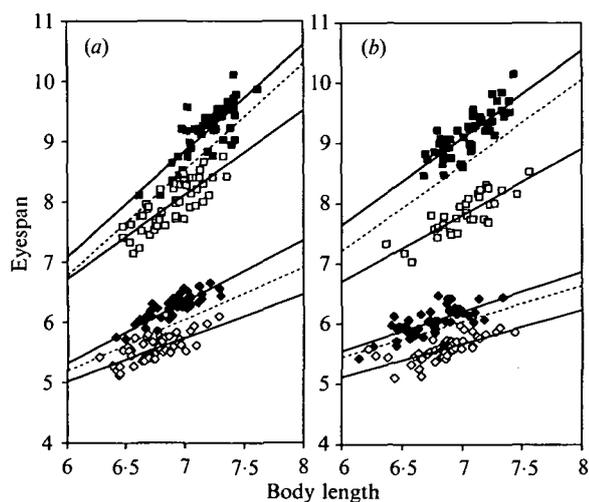

Fig. 3. Change in static allometric relationships as indicated by a plot of eye span against body length (mm) for (a) replicate 1 and (b) replicate 2 after 10 generations of selection. In each panel the filled points and associated least squares regression lines represent the increased ratio lines, the open points indicate the decreased ratio lines and the dashed lines the unselected lines. Boxes correspond to males and diamonds to females.

the duration of the experiment. Although pupal production was not assessed every generation, the rate of pupal production within each line appeared to increase as the experiment progressed.

Table 4. *F-ratios and squared correlation coefficients from ANCOVAs on eye span measured after 10 generations of selection with body length as a covariate*

Source	D.F.	Males†	Females†
Treatment	1	2·2	0·5
Body length	1	613·2**	387·7**
Replicate within treatment	1	20·2**	3·2*
Treatment × body length	1	4·2*	1·8
R^2		0·89	0·81

* Significant at 5%; ** significant at 0·1%.
† Sample size for males = 184 and for females = 200.

Comparison of eye span on body length regressions between selected lines for males and females after 10 generations of selection revealed that the static allometric relationships between eye span and body length changed as a correlated response to selection on relative eye span (Fig. 3). The slopes of the least squares regression lines differ between high and low lines for males as indicated by a significant treatment-by-body length interaction in an ANCOVA on eye span in which replicate is nested within treatment and body length is a covariate (Table 4). The means of the replicate lines also differed within treatments.
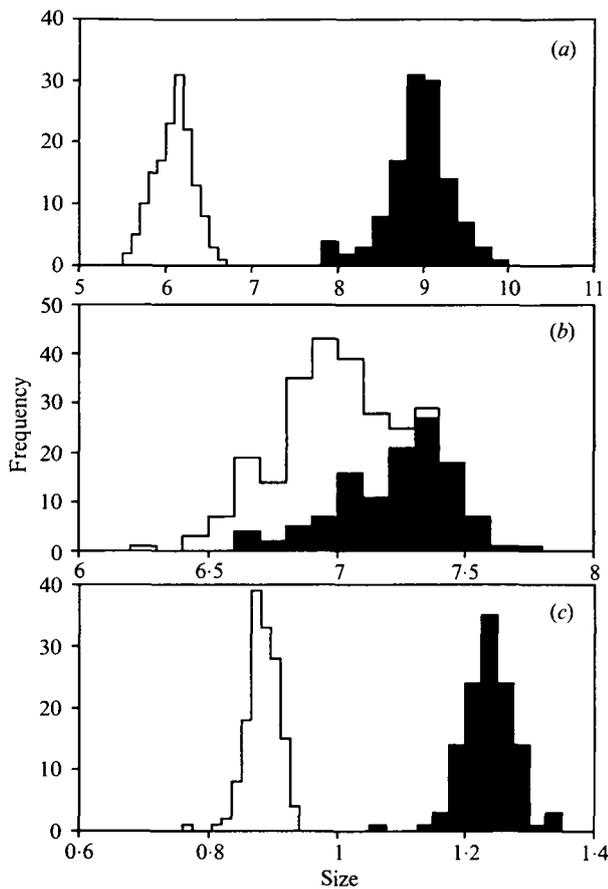
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Fig. 4. Frequency histograms of (a) eye span (mm), (b) body length (mm) and (c) the ratio of eye span to body length for males (shaded bars) and females (open bars) prior to selection in generation one.
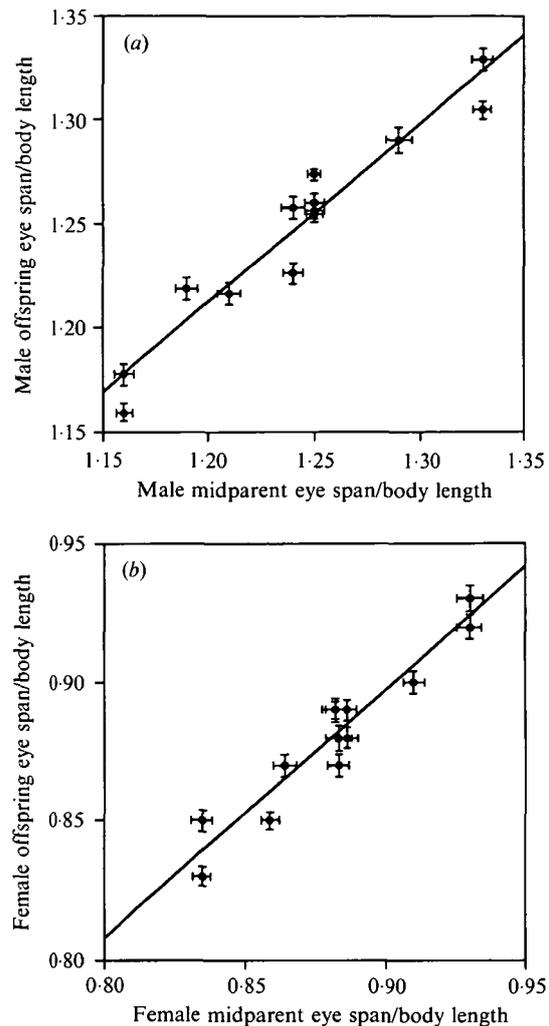

Fig. 5. Plots of average offspring against average parental eye span to body length ratio for (a) 50 male parents and 50 male offspring and (b) 25 female parents and 25 female offspring from crosses between pairs of selected lines after 13 generations of selection.

Although the two high lines have similar allometric slopes and intercepts, the L2 line has a lower intercept and shallower slope than the L1 line for both sexes (Fig. 3), as expected given the higher heritability for relative eye span in the L2 than the L1 line (Table 3).

(ii) *Additive gene action*

Prior to the onset of selection absolute and relative eye span distributions did not deviate from normality (Fig. 4). However, the distribution of body lengths (Fig. 4) exhibited negative skew in both sexes (male skew $= -0.68$, $n = 120$, $P = 0.0037$; female skew $= -0.38$, $n = 150$, $P = 0.0017$, Kolmogorov–Smirnov one-sample test for normality). After 10 generations of selection negative skew was significant when averaged across the six replicate line distributions of male eye span (skew $= -0.32$, one-sample $t = -3.55$, $P = 0.016$) and of male body length (skew $= -0.41$, one-sample $t = -5.26$, $P = 0.003$). Although the average skew across the six lines in male relative eye span did not differ from zero (skew $= -0.06$, one-sample $t = -0.72$, $P = 0.50$), male relative eye span in one of the unselected lines exhibited positive skew. After

excluding the two unselected lines, average skew for male relative eye span among the four remaining selected lines was less than zero (skew $= -0.15$, one-sample $t = -3.97$, $P = 0.029$). Average skew in female distributions across lines, in contrast, did not differ from zero for any trait. Average kurtosis across lines differed from zero only for male relative eye span (mean $= -0.60$, one-sample $t = -3.31$, $P = 0.02$).

To determine if the nonnormal phenotypic distributions of generation 10 males were due to non-additive environmental or genetic effects, flies between lines were crossed after 13 generations of selection. For each cross 25 randomly selected virgin males from one line were placed in a cage with 25 randomly selected virgin females from the other replicate of either the same or a different selected line. Flies from twelve pairs of lines were crossed and at least 25 progeny of each sex were measured. The least squares regressions of eye span to body length ratio for the average offspring on the same ratio for average parent
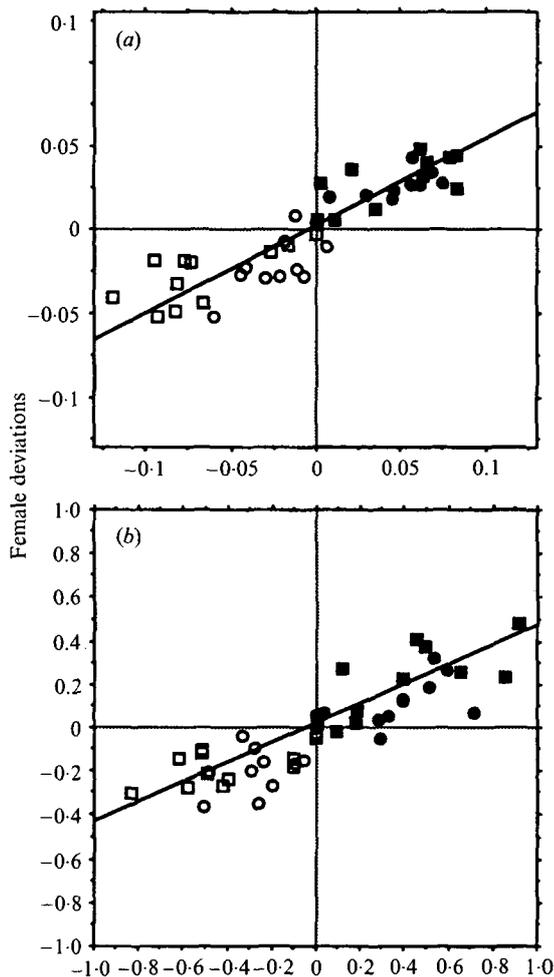
Fig. 6. Correlated response in females indicated by deviations from unselected lines for females plotted against deviations from unselected lines for males for (a) the ratio of eye span to body length and (b) eye span. Each point refers to the difference in mm between mean values each generation. Lines represent a least squares fit to the pooled data from all four selected lines. Filled symbols indicate high line differences while open symbols represent low line differences.
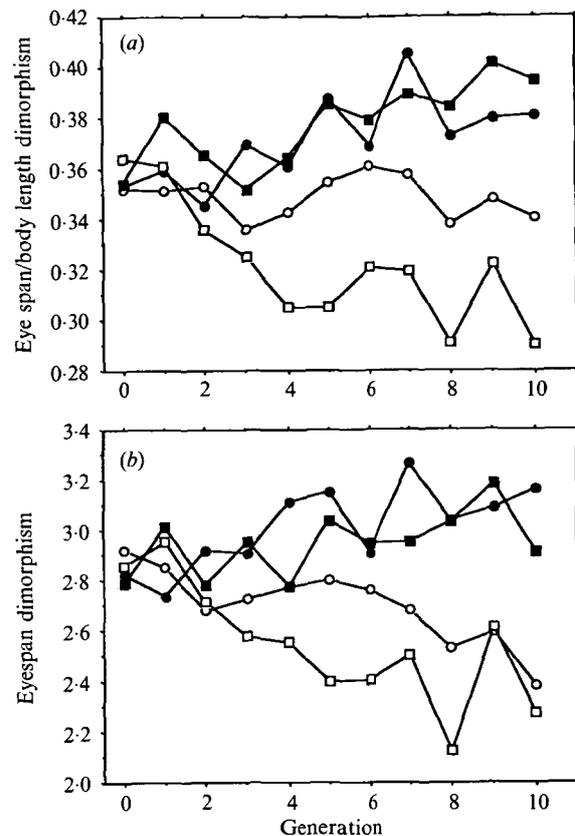

Fig. 7. Change in sexual dimorphism as indicated by the difference between male and female mean (a) ratio of eye span to body length and (b) eye span plotted against generation number.

were highly significant and obviously linear for both sexes ($P < 0.001$, Fig. 5). The regression equation for males was $y = 0.86x + 0.18$ ($r^2 = 0.93$) and for females it was $y = 0.89x + 0.09$ ($r^2 = 0.92$).

The two pairs of reciprocal crosses involving the high and low lines provide no evidence of maternal effects or sex linkage on relative eye span. The average absolute difference between the two reciprocal crosses of high and low lines did not differ from zero (average male difference $\pm$ S.E. $= 0.013 \pm 0.008$; average female difference $\pm$ S.E. $= 0.002 \pm 0.008$). Thus, genes influencing relative eye span in the high and low lines act independently of sex.

(iii) *Effects on sexual dimorphism*

The correlated response in relative and absolute eye span among females indicates a genetic correlation between male and female eye span. Because I did not exert selection on females, I cannot measure the heritability of female traits (Falconer, 1981). However, under the assumption that the heritability of a female trait equals that of the corresponding male trait, the genetic correlation between the sexes equals the slope of the regression of female deviation on male deviation for each selected line (Lande, 1980). Using this method the genetic correlation does not differ between lines ($F = 3.4$, $P = 0.35$; ANCOVA). The average ($\pm$ S.E.) genetic correlation between males and females for relative eye span is 0.39 ± 0.07 and for absolute eye span it is 0.29 ± 0.05 (Fig. 6). Standard errors were obtained directly from the four estimates.

Sexual dimorphism for absolute eye span has increased in the high lines and decreased in the low lines (Fig. 7). After 10 generations of selection the average difference between the sexes in absolute eye span is 3.04 mm while it is only 2.33 mm in the low lines ($t = 5.22$, $P = 0.035$) and 2.66 mm in the unselected lines. Average sexual dimorphism has not changed significantly between the high and low lines for relative eye span ($t = 2.74$, $P = 0.11$), body length ($t = 0.73$, $P = 0.54$), or thorax width ($t = 3.11$, $P = 0.09$). Sexual dimorphism has increased more for absolute than for relative eye span presumably because, as noted above, the genetic correlation

between the sexes is less for absolute than for relative eye span.

4. Discussion

Despite evidence for directional selection being exerted on relative eye span by male mating success (Wilkinson & Reillo, in prep.), the results of this study demonstrate that sufficient additive genetic variation is available for relative eye span in *C. dalmanni* to respond to selection. The symmetrical responses observed to bidirectional selection indicate, in contrast to predictions, that the genes influencing relative eye span are not at extreme frequencies, do not exhibit strong directional dominance, and are as likely to increase, as decrease, the expression of the trait. The strong linear relationships between offspring and parental means from crosses between selected lines provide additional evidence that many autosomal genes have additive effects on relative eye span. Correlated responses in the static allometric relationships between eye span and body length indicate that additive genetic variation also exists for static allometry. While a few other studies have demonstrated heritable variation in static allometric relationships (Robertson, 1962; Cock, 1969; Weber, 1990), this study is unique because the eye span–body length allometric relationship is a conspicuous morphological feature that often distinguishes between sexes and species of diopsids (Burkhardt & de la Motte, 1985) and functions in mate selection (Burkhardt & de la Motte, 1988; Wilkinson & Reillo, in prep.). Maintenance of morphological differences between sexes and species in the presence of additive genetic variation and strong sexual selection requires that some unidentified selective force opposes sexual selection.

Opposing selection may affect larval or pupal survival among flies with high breeding values for relative eye span. Because genetically larger flies take longer to develop (Robertson, 1960; Partridge & Fowler, 1993), they are exposed to higher concentrations of toxic metabolites from conspecific larvae (Botella *et al.* 1985) as well as to parasites and predators over longer periods. Three observations on *C. dalmanni* in the lab are consistent with this hypothesis. (1) High line flies take almost one day longer to develop than unselected or control line flies after 10 generations of selection (unpublished data). (2) Large pupae eclose less often than intermediate-sized pupae (P. Reillo, *personal communication*). Some *C. dalmanni* larvae carry millions of trypanosome (genus *Leptimonas*) parasites in their intestinal tracts (unpublished data). Because the eggs of these parasites are ingested as the fly larvae feed, time spent as larvae should correlate with degree of infection and possibly survival. (3) Body size declined in the unselected lines as expected if natural selection in the lab favors smaller body sizes.

At least two explanations other than direct negative selection on body size could account for a reduction in body size. First, the larval environment may have changed progressively to cause a nonheritable reduction in body size. This could happen if female fecundity or larval survival increased in each selected line over the course of the experiment. Increased larval competition results in smaller bodied flies in *Drosophila* (Atkinson, 1979) and in diopsids (unpublished data). Second, maternal effects could cause a heritable reduction in body size if selection for early fecundity caused a correlated decrease in egg size. These two possibilities could be tested by comparing age of first reproduction, egg size, and fecundity between selected line flies to flies recently captured in the field but reared in a standard environment.

The observation of negatively skewed male eye span distributions after selection supports the hypothesis that viability selection operates against males with above average length eye span. However, if this were true, then the negative skew should disappear as males are selected to have smaller eye span over successive generations. This result is not yet apparent, although tests of the normality of distributions within individual lines need to be conducted on much larger sample sizes to determine if any change in skew has occurred.

The negatively skewed phenotypic distributions, in conjunction with the linear relationship between parental and progeny means from crosses between lines, indicate that environmental variation is greater among small than large flies. In other words, breeding values are normally distributed but environmental effects are negatively skewed. Male flies reared under relaxed larval competition conditions are consistent with this explanation because they average 8·5 mm in eye span yet can produce male offspring that range in eye span from 3·5 to 10·5 mm when the larvae have variable access to food (unpublished observations). Thus, environmental effects can reduce more than increase eye span. In the field, male eye span ranges from 3·5 to 10·5 mm (Wilkinson & Reillo, in prep.) indicating much greater environmental variation influencing larval development in the field than in this selection experiment. Heritabilities estimated in this study must, therefore, overestimate heritabilities for these traits in the wild (Prout & Barker, 1989; Riska *et al.* 1989). However, in the absence of genotype-environment interactions (Gillespie & Turelli, 1989), the additive genetic variation demonstrated in this study should allow response to selection unless opposed by other selective forces.

The results reported here are consistent with the hypothesis that sexual dimorphism for relative eye span in *Cyrtodiopsis*, and possibly other diopsid genera, arose due to sexual selection on relative male eye span and is currently maintained by net stabilizing selection. Because the allometric relationship between eye span and body length among females exhibited a correlated response to selection on male relative eye span, female *C. dalmanni* and *C. whitei* would not be

expected to resemble male and female *C. quinque-guttata* (Burkhardt & de la Motte, 1985) unless stabilizing selection also acted to maintain the female eye span–body length allometric relationship. These results agree with others (Robertson, 1962; Cock, 1966; Weber, 1990) indicating that static bivariate allometric relationships can be altered by selection. However, because the static allometric relationships became steeper among males in the lines selected for increased relative eye span, much like the difference between males of sexually monomorphic and dimorphic species, static allometry may exhibit constrained evolutionary response.

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