Female Choice Response to Artificial Selection on an Exaggerated Male Trait in a Stalk-Eyed Fly

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Female choice response to artificial selection on an exaggerated male trait in a stalk-eyed fly

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SUMMARY

Quantitative genetic models for the evolution of exaggerated male traits through female mate choice predict that selection on male ornaments should cause a correlated response in female preferences. Furthermore, female selectivity should be inversely related to costs of mate choice. Here we use a stalk-eyed fly, *Cyrtodiopsis dalmanni* (Diptera: Diopsidae), which exhibits pronounced sexual dimorphism in eye span, to evaluate these predictions. Field observations reveal that each evening females aggregate while males disperse among roosting sites where mating occurs. A positive regression between male relative eye span and the number of females in an aggregation suggests that sexual selection acts on male eye span. Mate choice experiments in the lab, using flies after 13 generations of bidirectional selection on male relative eye span, reveal that females from long eye-span lines and an unselected population preferred long eye-span males. Short eye-span line females, however, preferred short eye-span males, demonstrating a genetic correlation between female preference and a sexually selected male trait. Eye span of the largest male in a field aggregation correlated positively with female age, as estimated by amount of eye pigment, and was independent of egg number, thereby providing no evidence that mate choice impairs female survival or fecundity.

1. INTRODUCTION

The evolution of exaggerated male traits by female mate choice is highly controversial (Kirkpatrick & Ryan 1991; Maynard Smith 1991). One view maintains that male ornaments coevolve with female preferences. Selecting an ornamented mate causes genes that influence expression of male trait and female preference to reside in the same offspring, creating linkage disequilibrium (Lande 1981; Kirkpatrick 1982). The magnitude of the resulting genetic correlation can influence evolutionary outcome. If the genetic correlation is high relative to the heritability of the male ornament, then a runaway process can occur (Lande 1981). Otherwise, the trait and preference increase until viability selection against further trait elaboration balances sexual selection. A genetic correlation between ornament and preference has also been assumed in some, but not all (Grafen 1990), good-genes models of the handicap principle (Zahavi 1977). Handicap refers to a costly male ornament that indicates viability. Evolution of female preferences for handicaps requires genetic variation for viability and depends on the magnitude of the genetic correlations between female preference, male ornament and viability (Iwasa *et al.* 1991). An alternative view holds that pre-existing sensory biases (Burley 1985; Ryan 1990) for conspecific recognition lead to trait exaggeration (Enquist & Arak 1993). Documenting genetic correlations between exaggerated male traits and female preferences provides evidence in support of coevolutionary models.

A second assumption which influences the outcome of male ornament evolution is whether mate choice influences female survival or fecundity. In the absence of selection on females, models of the Fisher process predict an equilibrium line between the male ornament and female preference (Lande 1981; Kirkpatrick 1982). If mate choice is under direct or correlated selection, however, either preferences will not evolve or a single equilibrium is predicted (Lande 1981; Pomiankowski 1987). Mate choice costs can be maintained in two ways: (i) females benefit directly by obtaining resources from a male or identifying a fertile conspecific (Kirkpatrick & Ryan 1991); and (ii) females benefit indirectly by receiving genes that improve offspring viability (Iwasa *et al.* 1991) or the sexual attractiveness of sons when mutation effects are biased (Pomiankowski *et al.* 1991). The degree of selectivity expected among females, i.e. the intensity of sexual selection, is expected to be inversely related to mate choice costs (Iwasa *et al.* 1991).

In this paper we use stalk-eyed flies, *Cyrtodiopsis dalmanni* (Diptera: Diopsidae), to document a genetic correlation between an exaggerated male trait and female preference and to demonstrate that females do not suffer increased mortality while choosing mates. We chose *C. dalmanni* for study because relative eye span provides an extreme example of sexual dimorphism (Burkhardt & de la Motte 1985) and is heritable (Wilkinson 1993). Eye-span sexual dimorphism is

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partly influenced by body size because the linear allometric relation between eye span and body length is steeper in males than females (Shillito 1971; Burkhardt & de la Motte 1985). However, bidirectional sexual selection on the ratio of male eye span to body length changed male eye span much more than body length, and altered the slope of the allometric relation between eye span and body length (Wilkinson 1993). Here, we use these selected lines to measure correlated responses in mate preference.

Previous work on Malaysian diopsids suggests that eye span influences mating success. During the day flies forage alone by grazing on rotting vegetative matter, but in the evening they move to streams and form aggregations on root hairs underneath banks where male competition and female choice can occur (Tan 1967; Burkhardt & de la Motte 1983). Males attempt to displace each other from hairs as aggregations form. Confrontations between males in the morphologically similar congener, *C. whitei*, are usually won by the male with the longest eye span (de la Motte & Burkhardt 1983; Burkhardt & de la Motte 1987). Female *C. whitei* also prefer to alight on strings containing model males with the longest eye span (Burkhardt & de la Motte 1988). Because mating occurs at dusk or dawn in aggregations (Burkhardt & de la Motte 1987; Lorch *et al.* 1993), we use field collections of *C. dalmanni* aggregations to estimate sexual selection on eye span and to determine if mate choice influences female survival or fecundity.

2. METHODS

Field work was done in peninsular Malaysia during January and October 1989. To measure the stability of site preferences over time, we counted males and females on 40 root hairs along 200 m of stream bank 36 km N of Kuala Lumpur (3° 19′ N, 101° 43′ E) on 23 January 1989 and again on 16 October 1989. To quantify sexual selection we collected flies at night roosting alone or in aggregations along streams 15 km W of Kuala Lumpur (3° 6′ N, 101° 48′ E) by enclosing all flies on a root hair with a nylon stocking. Live flies were frozen in liquid nitrogen in the field and kept to −80 °C until processed for size and age.

In the laboratory, each fly was scored for eye span, body length, age and, if female, fecundity. Eye span and body length from face to wing tip were measured to the nearest 0.1 mm with a video digitizing system (Wilkinson 1993). The number of mature oocytes within the abdomen of each female was counted after dissection. Age was estimated from the amount of pteridine eye pigments (Lehane *et al.* 1986; Lehane & Hargrove 1988). Recently thawed fly heads were homogenized for 60 s with a tissue grinder in 3 ml 0.1 N NaOH buffer adjusted to pH 10 with glycine, vortexed for 30 s, and the supernatant measured for relative fluorescence in a fluorospectrophotometer with the excitation and emission monochromators set at 350 nm and 450 nm, respectively. Two tetraphenylbutadiene cells were used to standardize relative fluorescence of samples: one after each sample, and one between measurement sessions. Readings were standardized to a fixed fluorescence value of the secondary standard.

To quantify the relation between relative fluorescence and age, flies were maintained on a 12 h light : dark cycle at 25 °C with a 30 min dawn–dusk period in vented Nalgene mouse cages (13 cm × 13 cm × 23 cm). Ground corn was provided as food twice each week (Wilkinson 1993). At intervals of about one week between 3 d and 79 d, and at 191 d of age, ten males and ten females were frozen at −80 °C. Flies were drawn randomly from a series of age categories when processed.

To determine if the number of females per male in an aggregation estimated mating success, two males with different eye spans and body lengths were aspirated into each of 24 mouse cages containing an average of five females. Males were selected arbitrarily from a population cage, and differed in eye span by 16 ± 2 (s.e.) % and body length by 12 ± 2 %. One male in each cage was marked on the thorax with typewriter correction fluid to identify individuals. All copulations for 30 min after dawn were counted and timed on two successive days.

Four experiments using pairs of males differing in eye span but matched for body length were conducted to quantify mate choice in the presence and absence of male interactions. Test males were created by artificial sexual selection in which 10 of 50 males with the longest (L) or shortest (S) eye span to body length ratio mated with 25 randomly chosen females, giving an effective population size of 29 each generation (Wilkinson 1993). In each experiment, sets of five females were aspirated into vented clear plastic cages (13 cm × 13 cm × 23 cm) with two hanging strings and two selected line males. After 2 d of acclimation, the number of females with each male before daylight was counted and averaged over a 7 d period. In the first experiment, 155 unselected line females were scored roosting on strings with males from lines after 9 ($n = 26$ pairs) or 13 generations ($n = 5$ pairs) of selection. Test male pairs differed in eye span by 0.97 ± 0.07 (s.e.) mm and in body length by 0.02 ± 0.02 mm.

In experiments 2–4, male competition was excluded by separating L and S line males after 13 generations of selection with clear acetate partitions perforated with 7 mm diameter holes. The partitions allowed females, but prevented males, from moving between cage sides, while still allowing flies to see each other. Experiment 2 tested 75 unselected females to document preference independent of male contact. Experiments 3 and 4 used females after 13 generations of artificial selection to determine if preferences responded to selection on male eye span. Experiment 3 tested 65 females from one L line replicate and 25 females from the other, whereas experiment 4 used 125 females from one S line replicate. In each experiment a unique pair of males was used to test the five females, but many of the same male pairs were used in experiments 2–4. The average difference between male pairs in eye span ranged from 1.57 mm to 1.47 mm, and in body length from 0.05 mm to 0.01 mm in experiments 2–4. Past association with males could not influence mate preferences because females from each selected line were caged together after eclosion without males until tested 2–3 months later. Food was available on both sides of the partition in all cages.

3. RESULTS

Examination of flies collected from 45 root hairs (Figure 1) revealed that females clustered while males dispersed beyond random expectations. The variance-to-mean ratio was 2.30 for females (Poisson expectation goodness-of-fit $\chi^2 = 10.9$, 3 d.f., $p = 0.012$) and 0.61 for males ($\chi^2 = 8.0$, 3 d.f., $p = 0.046$). If female aggregations are a consequence of fixed site preferences, then the same sites should consistently contain more females. In contrast, the correlation between two nocturnal counts separated by 10 months was only 0.23 for females (157 and 85 individuals, $p > 0.05$) but 0.41

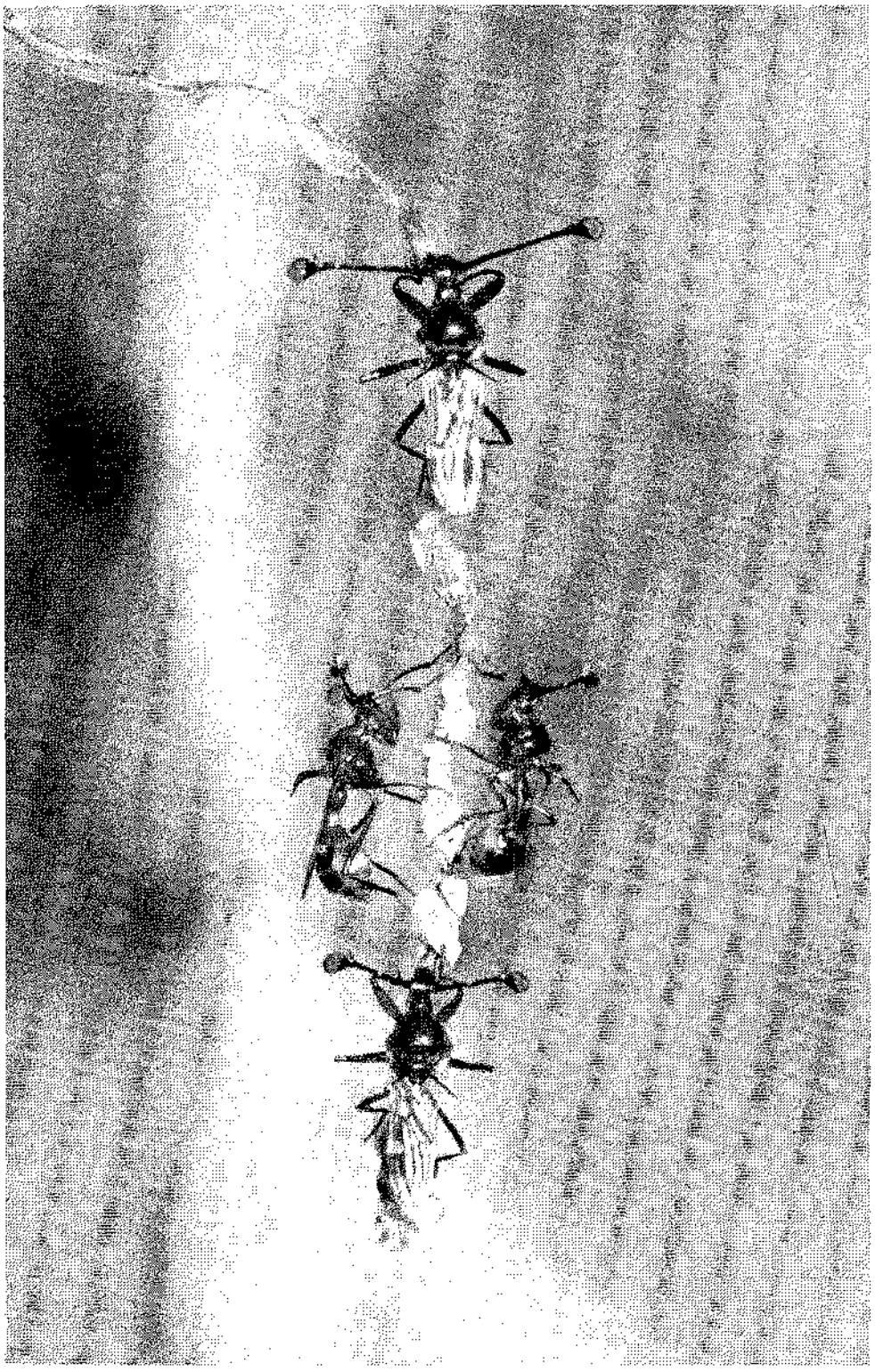

Figure 1. Nocturnal aggregation of *C. dalmanni* on a root hair in peninsular Malaysia. The male above three females has an eye span of 9.2 mm.

for males (63 and 73 individuals, $p < 0.01$). Female aggregations do not, therefore, appear to be determined by microhabitat choice alone.

The average number of females per male increased with male eye span in field-collected aggregations. Unfortunately, the collinearity between male eye span and body length ($r = 0.96$, $n = 102$, $p < 0.0001$) confounded attempts to use multiple regression (Lande & Arnold 1983) to estimate selection on eye span independent of body size. To partly control for the effects of body size, we regressed the average number of females per male against the ratio of male eye span to body length (figure 2). The regression explained a significant fraction of variation in relative mating success ($r^2 = 0.22$, $F = 9.90$, d.f. = 1,43, $p = 0.001$). The selection intensity (Lande & Arnold 1983), estimated by the covariance between relative number of females per male and male eye-span ratio divided by

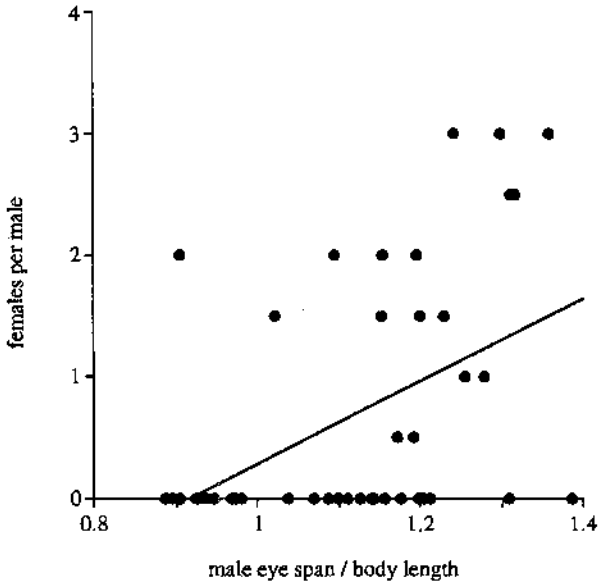

Figure 2. Plot of number of females roosting with each male at night and the ratio of male eye span to body length. The line represents the least squares regression, $y = -3.13 + 3.42x$.

the standard deviation in male eye-span ratio, was 0.69, more than half that exerted each generation during experimental sexual selection (Wilkinson 1993).

Observations in captivity support using number of females per male on a root hair to estimate mating success because females mate in aggregations. On average, 4.7 ± 1.9 (s.d.) copulations occurred within 30 min after daylight, i.e. most females mated each morning. The larger male obtained 57% of 226 copulations, which lasted an average of 51.4 ± 18.9 (s.d.) s. Mating success may be less skewed in cages than in the field because in cages females could not evade males, and large males could not exclude small males.

In the first mate choice experiment both male competition and female choice could have occurred because males were free to interact. In 24 of 31 cages, more unselected females roosted with L males (figure 4; Wilcoxon signed-ranks test, $z = 3.43$, d.f. = 30, $p = 0.0003$), suggesting that either male competition, female choice or both occurred.

In experiments 2–4, male competition was excluded by a perforated partition separating males. In experiment 2, unselected females in 12 of 15 cages preferred L males (figure 4; Wilcoxon signed-ranks test, $z = 2.13$, d.f. = 14, $p = 0.033$), demonstrating female choice for eye span. In experiment 3, L females in 15 of 18 cages preferred L males (figure 4; Wilcoxon signed-ranks test, $z = 2.82$, d.f. = 17, $p = 0.005$), but, in experiment 4, S females in 16 of 25 cages preferred S males (figure 4; Wilcoxon signed-ranks test, $z = 2.27$, d.f. = 24, $p = 0.023$). Because many of the male pairs were identical in experiments 3 and 4, we tested for an effect of selected line on female preference directly. Comparison of matched differences in number of females from each selected line with L against S males revealed that selection on male eye span influenced female mate choice (Wilcoxon signed-ranks test, $z = 2.85$, d.f. = 17, $p = 0.003$).

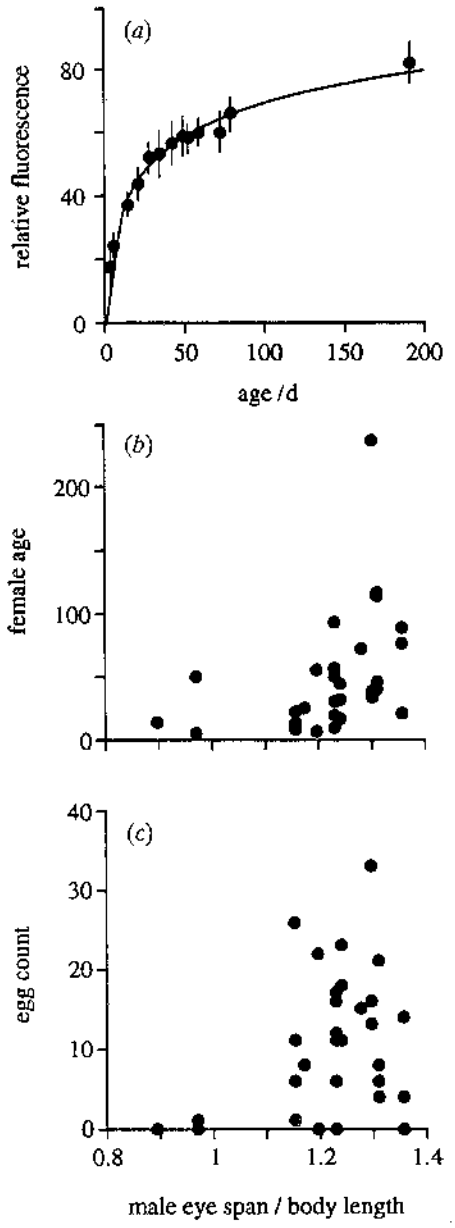

Figure 3. (*a*) Plot between relative fluorescence (mean $\pm$ 1 s.d.) of pteridine eye pigments and age of flies maintained in captivity. The line indicates the least-squares regression of relative fluorescence on log age, $y = 0.50 + 14.85x$. Relative fluorescence, after controlling for log age, was independent of sex (analysis of covariance, $F = 0.13$, d.f. = 1,232, $p = 0.72$). (*b*) Plot of female age against eye span/body length of the largest male in an aggregation. (*c*) Plot of number of mature eggs per female and eye-span ratio of the largest male in aggregation.

Because more than one male often roosted within 1 m of a female aggregation in the field, females could potentially compare males before selecting an aggregation site (Burkhardt & de la Motte 1983). If it is more costly for females to select large eye-span males than to mate at random then a negative correlation should exist between the relative eye span of the largest male in an aggregation and either female age or fecundity. We estimated age from flies captured in aggregations in the field by using the relation between average relative fluorescence of pteridine eye pigments and age of captive flies (figure 3*a*; $r^2 = 0.88$, $F = 1669$,

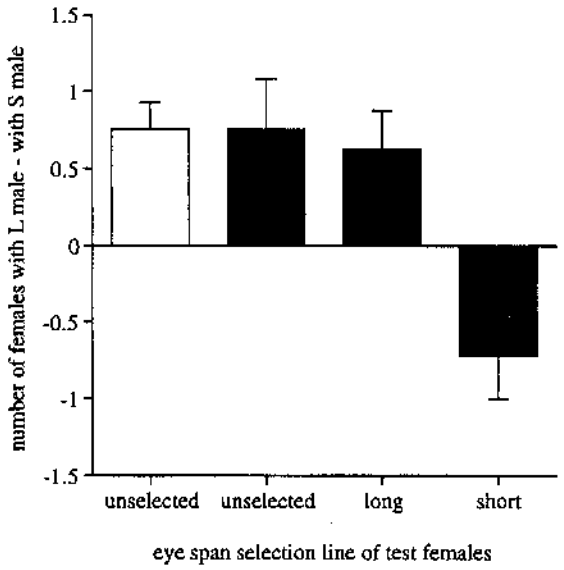

Figure 4. Difference between the number of females (mean ± s.e.) roosting either with an L or S male in the four mate choice experiments referred to in the text. Unfilled bar indicates experiment 1 where males could interact. Filled bars indicate, from left to right, experiments 2–4 in which a transparent perforated partition separated L and S males in each cage.

d.f. = 1,238, $p < 0.0001$). In contrast to prediction, female age correlated positively with eye-span ratio of the largest male in an aggregation (figure 3*b*; Spearman rho = 0.59, $n = 31$, $p = 0.001$). The correlation between eye-span ratio of the largest male and female egg count was not significant (figure 3*c*; Spearman rho = 0.22, $n = 31$, $p = 0.25$). Furthermore, females captured while roosting alone did not differ in age from females captured in aggregations ($t = 0.05$, d.f. = 8,36, $p = 0.95$). Selecting an aggregation does not, therefore, appear to impair female survival.

4. DISCUSSION

Our results suggest that *C. dalmanni* female mate preference changed as a consequence of artificial selection on male relative eye span. Because females were housed separately from males, and selection was not exerted on females, we interpret the changes in female preference to result from a genetic correlation between male eye span and female preference (Falconer 1981). These results are consistent with coevolutionary models of female choice sexual selection.

If a genetic correlation exists between male eye span and female preference, then selection for increased eye span should produce more choosey females. However, we observed no difference in preference between unselected and L line females. At least three explanations for this apparent asymmetry are possible: (i) preference for long eye-span males has reached a ceiling among unselected females; this suggestion seems doubtful given that females rarely exhibited unanimous choices; (ii) the genetic correlation between trait and preference was higher among S than L line flies; genetic drift is a possible, but questionable, mechanism for such a difference; and (iii) preferences differ between L and unselected line females, but went undetected because suitable test males were not provided. If L line females preferred longer eye-span males than offered, then no difference in preference might be measured. Mate choice experiments on *C. whitei* support this interpretation because females preferred model males with longer eye spans than exist in natural populations (Burkhardt & de la Motte 1988).

Two recent studies provide evidence that female choice is heritable and may covary genetically with male traits in other taxa. Mate choice experiments using the two-spot ladybird show that heritable female preference only occurs in areas where melanic forms are common (O'Donald & Majerus 1992), as expected if melanism correlates with female preference. A breeding study on sticklebacks has estimated a significant genetic correlation between male belly colour and female courtship intensity (Bakker 1993). However, the heritability for neither male coloration nor female preference differed significantly from zero. Furthermore, because female preferences were scored using only seven males (Bakker 1993), differences among test males unrelated to coloration could have influenced female courtship during preference tests. Because male sticklebacks provide parental care, and belly coloration indicates physical condition (Milinski & Bakker 1990), survival of offspring from females mating with ornamented males may be enhanced. Sticklebacks could, therefore, represent a case where direct benefits of mate choice led to linkage disequilibrium between trait and preference.

In contrast, no direct benefits of mate choice in stalk-eyed flies have been identified even though the positive correlation between female age and eye span of the largest male in an aggregation appears to show that mate choice improves female survival. Other causes for this correlation are, however, possible. For example, female ability to perceive differences among males may improve with age. If males return to common sites, as the significant correlation between number of males at sites over a 10 month period suggests, and females sample more sites as they age, then a correlation between male eye span and female age could result.

Although male stalk-eyed flies transfer sperm in a spermatophore (Kotrba 1990), *C. dalmanni* spermatophores are poorly designed to transfer resources to females. *C. dalmanni* and *C. whitei* produce gourd-shaped spermatophores which temporarily block spermathecal ducts but occupy only a part of the anterior vaginal cavity (Kotrba 1993). In contrast, a single spermatophore from at least one diopsid completely fills the vaginal cavity (M. Kotrba, personal communication). Female *C. whitei* eject a spermatophore within 1 h of copulation, often before it is empty (Kotrba 1993). Male *C. whitei* shorten copulation duration and avoid transferring sperm to females that have recently mated, presumably because first-male sperm precedence would prevent fertilization (Lorch *et al.* 1993). *C. dalmanni* also exhibit some short copulations (G. S. Wilkinson & P. R. Reillo, unpublished observation). Frequent mating opportunities for *C. dalmanni* males may have favoured a reduction in spermatophore volume (M. Kotrba, personal communication) and behavioural mechanisms for avoiding

sperm waste. Although this evidence does not exclude the possibility that females use eye span to assess spermatophore size, seminal nutrients are unlikely to account for much of the variation in female survival or fecundity (figure 4).

Although our results do not allow discrimination between good genes and Fisherian models for the evolution of male ornaments, presence of a genetic correlation between male ornament and female preference in the absence of direct or correlated selection on the preference is expected to lead to an equilibrium line (Lande 1981; Kirkpatrick 1982). Isolated populations of *C. dalmanni* could, therefore, differ in relative eye span as a consequence of genetic drift (Lande 1981). Interestingly, differences in average eye span among male *C. dalmanni* from Java and Sumatra have been reported (Shillito 1971). More systematic population sampling, coupled with estimates of genetic correlations between viability and mate preference, are needed to determine the relative contribution of good genes effects to the Fisher process in explaining the evolution of exaggerated male traits.

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