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# Exaggerated male eye span influences contest outcome in stalk-eyed flies (Diopsidae)

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**Abstract** Evolution of male weapons or status signals has been hypothesized to precede evolution of female mating preferences for those traits. We used staged male fights among three species of Malaysian stalk-eyed flies (Diptera: Diopsidae) to determine if elongated eye span, which is preferred by females in two sexually dimorphic species, influences contest outcome. Extreme sexual dimorphism, with large males possessing longer eye span than females, is shared by *Cyrtodiopsis whitei* and *C. dalmanni*. In contrast, *C. quinqueguttata* exhibits a more ancestral condition – short, sexually monomorphic eye stalks. Videotape analysis of 20-min paired contests revealed that males with larger eye span and body size won more fights in the dimorphic, but not monomorphic, species. To determine if males from the dimorphic species use eye span directly to resolve contests, we competed male *C. dalmanni* from lines that had undergone artificial selection for 30 generations to increase or decrease eye span. We found that eye span, independently of body size, determines contest outcome in selected-line males. Furthermore, in both dimorphic species, the average encounter duration declined as the eye span difference between contestants increased, as expected if males use eye span to assess opponent size. The number of encounters also increased with age in dimorphic, but not monomorphic, species. Selected-line males did not differ from outbred males in either fight duration or number of encounters. We conclude that exaggerated male eye stalks evolved to influence both competitive interactions and female mating preferences in these spectacular flies.

**Key words** Assessment · Intraspecific competition Sexual selection · Diopsidae

## Introduction

In a provocative paper, Berglund et al. (1996) argue that male secondary sexual traits often exhibit dual function, i.e., they attract mates and resolve contests either by acting as weapons or status signals. Support for this claim comes from a survey of studies on visual, acoustic, chemical, and electric signals which indicates that many signals influence both female mating preferences and contests among males. This idea has been suggested before (e.g., Fisher 1958; Borgia 1979; West-Eberhard 1979). Berglund et al. (1996) point out that conspicuous, costly signals used by males to resolve disputes over limiting resources, such as food and mates, provide females with honest indicators of male quality (Kodric-Brown and Brown 1984; Grafen 1990). Therefore, females should benefit most by choosing males on the basis of their weapon or status signal. If this proposition is correct, then the evolution of traits which resolve contests should precede the evolution of female preferences – a prediction directly opposite to sensory exploitation (Basolo 1990; Ryan et al. 1990; Ryan and Keddy-Hector 1992).

In this paper, we test the prediction that a male ornament preferred by females is also used in male-male competition as an assessment signal of body size. To evaluate this idea, we staged fights among males from three closely related species of Malaysian stalk-eyed flies (Diptera: Diopsidae) which differ in the degree of sexual dimorphism for eye span. All three species exhibit a high correlation between eye span and body size (Burkhardt and de la Motte 1985; Wilkinson and Dodson 1997), but in both dimorphic species, the slope of a linear least-squares regression between eye span and body size is much greater in males than females. In these two sister species, eye span ranges from 4 to 11 mm in males and

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4–6 mm in females. In contrast, no sexual dimorphism for eye span exists in *Cyrtodiopsis quinqueguttata*. In both sexes, the eye span on body length least-squares regression slope is <1 and eye span ranges from 3 to 5 mm (Wilkinson and Dodson 1997). The steeper male allometric slopes in the dimorphic species permit eye span to signal male size more accurately than in the monomorphic species (Petrie 1988; Green 1992; Eberhard et al. 1998). Phylogenetic reconstruction using mtDNA sequences indicates that *C. quinqueguttata* lies basal to *C. whitei* and *C. dalmanni*, and sexual monomorphism for eye span is plesiomorphic (Wilkinson et al. 1998a). Furthermore, mate choice experiments indicate that female *C. whitei* and *C. dalmanni*, but not *C. quinqueguttata*, prefer to mate with males with a larger eye span (Wilkinson et al. 1998a). Thus, if exaggerated eye stalks evolved to function in contest resolution, then eye span should influence fight outcome only in sexually dimorphic species.

Eye stalks have been implicated in contest resolution in several independent lineages of flies (Wilkinson and Dodson 1997). *Drosophila heteroneura* (Diptera: Drosophilidae) males with wider heads win more fights (Boake et al. 1997). *Achias australis* (Diptera: Platystomatidae) males with large eye span defend presumed mating sites (McAlpine 1979). In *C. whitei* (Diptera: Diopsidae), larger-eye-span males won over 90% of fights staged over mating sites in the laboratory (Burkhardt and de la Motte 1987). While these results suggest some role for eye stalks in fight resolution, they are also consistent with larger males displacing smaller males, as occurs in many invertebrates, e.g., earwigs (Radesater and Halldorsdotter 1993), jumping spiders (Faber and Baylis 1993), caddisfly larva (Englund and Olsson 1990), and crickets (Hack 1997), because eye span correlates with body size in all stalk-eyed flies (McAlpine 1979; Burkhardt and de la Motte 1985; Grimaldi 1987; Grimaldi and Fenster 1989). In many holometabolous insects, the expression of adult secondary sexual traits often covaries allometrically with body size because development of the trait depends on how much food a larva consumes before pupation (Emlen 1994; Nijhout and Emlen 1998). Consequently, an association between eye span and fight outcome could occur for two reasons. (1) Body size, independent of eye span, determines fights. In this case, the apparent effect of eye span on fight outcome is due to an incidental phenotypic correlation between eye span and body size. (2) Eye span directly determines the outcome of a fight because body size is assessed from eye span.

We used two approaches to determine if eye span, independent of body size, is causally related to fight resolution. The first approach relies on experimental manipulation of the sexually selected trait independent of body size, as has been done for snapping shrimp (Hughes 1996). We staged fights between *C. dalmanni* males from lines which had undergone artificial selection to increase or decrease the ratio of eye span to body length for 30 generations (Wilkinson 1993). Selection on this ratio altered eye span much more than body size (Wilkinson 1993) making it possible to compete males which differed greatly in eye span but not in body size. The second approach involves testing a prediction from game theoretic models of fighting behavior (Parker 1974; Enquist and Leimar 1983), i.e., fight duration should be inversely related to the degree of difference in the trait under assessment between opponents (Englund and Olsson 1990; Enquist et al. 1990; Leimar et al. 1991). Consequently, we compared fight duration against difference in opponent eye span for each of the three species. A decrease in fight duration with an increase in the degree of difference in eye span between opponents would be consistent with direct assessment of eye span.

## Methods

### Staging fights

To create males of different sizes, we allowed stock population females of each species to lay eggs in cups containing 50 ml of pureed corn media (Wilkinson 1993) for 3–4 days. Each population was housed in a large plexiglass cage lined with moist blotting paper and cotton and contained 100–200 adults. We allowed larvae to develop at 25 ± 0.1 °C with a 12-h light:dark cycle. Under these conditions, larvae develop into adult flies with a range of body sizes due to larval competition (G.S. Wilkinson, personal observation). After eclosion, we separated males from females and housed no more than 25 individuals of the same age and species in ventilated polycarbonate cages (13 × 13 × 20 cm). At least 24 h prior to a contest, we anesthetized flies with carbon dioxide to mark their thorax uniquely with a paint pen. We also used NIH Image, version 1.59, to measure eye span, body length, and thorax width to the nearest 0.01 mm from a video-captured image of each fly under a microscope.

We staged fights from 0900–1100 hours using males matched for age. Flies ranged in age from 30 to 90 days. All three species are sexually mature at least 2 weeks after eclosion and longevity in the laboratory and the field can be 6 months or more (Wilkinson and Reillo 1994; Wilkinson and Dodson 1997). Flies were only allowed to compete once. We used food, rather than females, to promote fights because, in contrast to the two sexually dimorphic species, *C. quinqueguttata* does not form nocturnal aggregations and shows no tendency to mate at dusk or dawn (Kotrba 1996). Preliminary observations on all three species revealed that paired males readily engaged in agonistic interactions after being deprived of food for 18 h and diurnal contests over food during the day closely resembled crepuscular contests over aggregations of females on rootlets in *C. whitei* (Burkhardt and de la Motte 1987) and *C. dalmanni* (Wilkinson and Reillo 1994). The day before each contest, we aspirated two marked males into a small (10 × 3.5 × 6 cm) polystyrene chamber lined with moist blotting paper and separated them using two removable opaque partitions. After 18–20 h without food, we placed a small drop of corn water and yeast between the partitions on the bottom of the chamber. We then removed the partitions and starting with the first interaction, we recorded the flies for 20 min using a Sony TR-81 Hi-8 camcorder. At the end of the recording period, we removed each fly and weighed it to the nearest 0.1 mg.

To determine if exaggerated eye span influences fighting success, we paired males to create a similar range of body length differences between opponents for each species. Under these culture conditions, males do not differ in body length between these species (Wilkinson et al. 1998a). We staged 29 *C. whitei*, 30 *C. dalmanni*, and 24 *C. quinqueguttata* contests. The mean (±SE) and range of differences in body length between paired males for each species was comparable (*C. whitei*: 0.55 ± 0.08, 0–1.54 mm; *C. dalmanni*: 0.40 ± 0.07, 0–1.40 mm; *C. quinqueguttata*: 0.34 ± 0.08, 0–1.50 mm) and the mean differences in body length did not differ between species (ANOVA: $F_{2,80}$ = 2.09, $P$ = 0.13). In contrast, the difference in eye span between opponents differed markedly between species (ANOVA: $F_{2,80}$ = 8.70, $P$ = 0.0004). Both sexually dimorphic species exhibited significantly greater differences in eye span than the sexually monomomorphic species (Fisher's protected least-squared differences test, $P$ < 0.005) but did not differ from each other (*C. whitei*: 0.94 ± 0.13, 0.02–2.47 mm; *C. dalmanni*: 0.72 ± 0.14, 0–2.74 mm; *C. quinqueguttata*: 0.23 ± 0.04, 0.03–0.79 mm).

The high correlation between male eye span and body length for all outbred populations (*C. whitei*: $r$ = 0.93, $P$ < 0.0001, $n$ = 58; *C. dalmanni*: $r$ = 0.89, $P$ < 0.0001, $n$ = 60; *C. quinqueguttata*: $r$ = 0.81, $P$ < 0.0001, $n$ = 48) precluded using multivariate statistics to determine if males use eye span independently of body size to assess opponents. Instead, we staged contests using *C. dalmanni* males from lines which had undergone artificial selection for 30 generations either to increase or decrease the ratio of eye span to body length (Wilkinson 1993; Wilkinson et al. 1998b). We staged 29 contests between selected-line males which were 50–150 days old and matched for age. The correlation between eye span and body length was much lower for selected-line ($r$ = 0.49, $P$ < 0.0001, $n$ = 58) than outbred *C. dalmanni* males used in contests. Consequently, by pairing long-eye-span-line males with short-eye-span-line males we more than doubled the average difference in eye span (1.89 ± 0.14, range: 0.6–3.68) without increasing the average or range of differences in body length (0.31 ± 0.06, 0–1.06 mm) between competitors.

### Scoring fights

Males of the sister species, *C. whitei* and *C. dalmanni*, used similar sequences of behaviors during contests. In both species, a contest initiated when two males oriented face to face and approached with parallel eye stalks and bobbing abdomens. If neither male retreated, then occasionally one male would jump on the other or spread, rotate and briefly display one or both wings. More often, both males rose on their hindlegs and extended their forelegs next to the eye stalks. If neither male retreated at this point, then fights would escalate with one male using forelegs to jab the face or hook a leg and upend the other fly. Occasionally, winners briefly chased retreating opponents. These behaviors were indistinguishable from those used by males fighting over females at aggregation sites (de la Motte and Burkhardt 1983; Burkhardt and de la Motte 1987; G.S. Wilkinson, personal observation).

*C. quinqueguttata* males exhibited fighting behavior similar to the other two species, but they more frequently displayed wing-spreading behavior following initial frontal orientation. Wing spreading was often accompanied by several quick lunging steps towards an opponent. If neither male retreated after a wing spread, encounters escalated to physical contact as described above for the two dimorphic species.

Because males of all three species used similar agonistic behaviors, we measured duration (to the nearest second) of an aggressive encounter beginning when the males faced each other and ending when one turned away. The male which did not retreat was scored the winner of an encounter. When both males turned away at the same time we scored the encounter as a tie. We did not include chases in the duration of an encounter because the point at which a male stopped pursuit was often ambiguous. The fly that won the most encounters during the 20-min period was the winner of the contest.

The amount of fighting we observed during a contest was due both to the duration of each aggressive encounter and to the number of times the two males encountered each other. These two components of fighting duration reflect different aspects of male behavior. Encounter duration should be influenced by the amount of time involved in assessing opponent size or fighting ability while number of aggressive encounters will vary depending on the general activity of each fly. Therefore, we compare these two aspects of fight duration separately below for the outbred populations of each species. Because assessment or activity could change with experience acquired in communal cages prior to paired contests, we also tested each fight duration variable for influence due to age.

We assessed the influence of contestant differences in predicting fight outcome using paired *t*-tests and binomial tests on each measure of size. To determine if eye span influenced fight outcome independently of body size for each of the four sets of contests, we compared winners and losers on the residuals from a regression of eye span on body length. To determine if fight duration was influenced by eye span difference, body length difference, age or species we used analysis of covariance (ANCOVA) on the natural logarithm of average encounter duration and on the number of encounters recorded in 20 min. The log transformation removed an association between the variance and mean of the average encounter duration.

## Results

### Determinants of fight outcome

Paired *t*-tests revealed that all four measures of male size differed significantly between winners and losers in *C. whitei* (eye span: $t$ = 3.25, $P$ = 0.003; body length: $t$ = 3.25, $P$ = 0.003; thorax width: $t$ = 3.51, $P$ = 0.002; body mass: $t$ = 2.20, $P$ = 0.037, *df* = 29) and *C. dalmanni* (eye span: $t$ = 3.96, $P$ = 0.0004; body length: $t$ = 2.92, $P$ = 0.007; thorax width: $t$ = 2.48, $P$ = 0.019, *df* = 28; body mass: $t$ = 3.40, $P$ = 0.002, *df* = 26). Eye span was the best predictor of contest outcome for both dimorphic species (Fig. 1a,b). In *C. whitei*, larger-eye-span males won 83% ($Z$ = 3.5, $P$ = 0.0004), larger-body-length males won 76% ($Z$ = 2.8, $P$ = 0.005), and heavier males won 69% ($Z$ = 2.0, $P$ = 0.041) of contests, while in *C. dalmanni*, larger-eye-span males won 77% ($Z$ = 2.9, $P$ = 0.0035), larger-body-length males won 62% ($Z$ = 1.3, $P$ = 0.19), and heavier males won 71% ($Z$ = 2.0, $P$ = 0.041) of contests.

In contrast to the sexually dimorphic species, paired *t*-tests revealed no significant differences between winner and loser male *C. quinqueguttata* for any of the four size measures (eye span: $t$ = 0.1, $P$ = 0.93; body length: $t$ = 0.4, $P$ = 0.70; thorax width: $t$ = 0.1, $P$ = 0.91, *df* = 23; body mass: $t$ = 0.25, $P$ = 0.37, *df* = 20). Winning male *C. quinqueguttata* had larger eye span in 58% ($Z$ = 0.8, $P$ = 0.41, Fig. 1c), larger body length in 63% ($Z$ = 1.2, $P$ = 0.22), and more mass in 48% of contests ($Z$ = 0.2, $P$ = 0.83). Body size did not, therefore, predict fighting success in the sexually monomorphic species.

To determine if eye span influences contest outcome independently of body size, we compared the residuals from the regression of eye span on body length for winners against losers for each of the three species (Fig. 1d,e). Neither paired *t*-tests on residual eye span between winner and loser nor binomial tests revealed significant differences for any species. This result can be explained in two possible ways. Either eye span

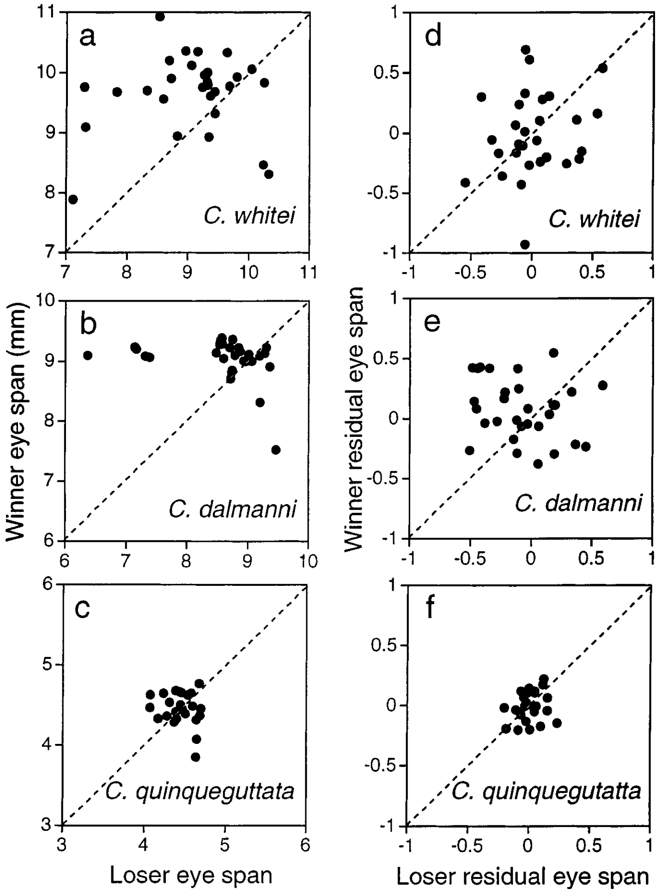

**Fig. 1** Outcomes of fights between outbred males of each species. Eye span of winners is plotted against losers for *Cyrtodiopsis whitei* (**a**), *C. dalmanni* (**b**), and *C. quinqueguttata* (**c**). Residuals from a regression of eye span on body length for winners are plotted against residuals for losers for *C. whitei* (**d**), *C. dalmanni* (**e**), and *C. quinqueguttata* (**f**). *Dashed lines* indicate equal eye span between winner and loser

functions as an accurate indicator of body size to resolve contests or males assess each other's size without relying on eye span. To distinguish between these alternatives, we staged contests using male *C. dalmanni* from lines in which eye span was altered through artificial selection. *C. dalmanni* selected-line males with larger eye span won 83% of trials ($Z = 3.5$, $P = 0.0004$; Fig. 2a). Seventy-six percent of the winners also had equal or larger body size ($Z = 2.8$, $P = 0.005$) but only 59% were heavier ($Z = 0.9$, $P = 0.35$). A plot of winners against losers (Fig. 2b) for eye span residuals from a regression of eye span on body length revealed that 79% of the winners had larger eye span relative to their body length ($Z = 3.2$, $P = 0.0016$). Furthermore, in 21 contests, the absolute difference in body length between the flies was less than 0.5 mm, yet the male with larger eye span still won 15 of these contests ($Z = 1.96$, $P = 0.0495$). These results provide strong evidence that eye span, independently of body size or mass, determines contest outcome in at least this sexually dimorphic species.

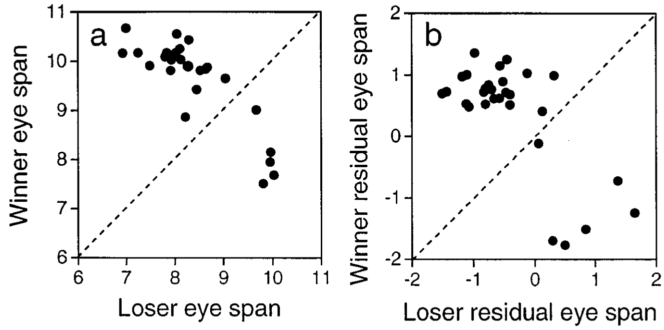

**Fig. 2** Outcomes of fights between selected-line *C. dalmanni* males: eye span of winners plotted against losers (**a**) and residuals from a regression of eye span on body length for winners plotted against residuals for losers (**b**). *Dashed lines* indicate equal eye span between winner and loser

## Determinants of fight duration

ANCOVA revealed that the average duration of an aggressive encounter was influenced both by the species ($F_{2,77} = 8.65$, $P = 0.0004$)and by the difference in eye span between the contestants ($F_{1,77} = 5.3$, $P = 0.0.024$) but not by the difference in body length ($F_{1,77} = 0.01$, $P = 0.93$) or age ($F_{1,77} = 0.63$, $P = 0.43$). No interaction term was significant in this model. The species effect was caused by longer encounters among *C. whitei* males than among either *C. dalmanni* or *C. quinqueguttata* males (least-squares means comparisons: *C. whitei* vs *C. dalmanni*: $t = 3.84$, $P = 0.0002$; *C. whitei* vs *C. quinqueguttata*: $t = 3.26$, $P = 0.0017$; *C. dalmanni* vs *C. quinqueguttata*: $t = 0.57$, $P = 0.57$). Average encounter duration for the two dimorphic species declined as the difference in eye span between the contestants increased, as expected if males engage in aggressive encounters for longer periods when assessment of opponent size is more difficult (Fig. 3).

The absence of a significant interaction in the ANCOVA between species and eye span difference indicates that the slope of the relationship between average encounter duration and difference in eye span did not differ between species. However, plots of encounter duration on eye span difference for each species (Fig. 3) revealed significant regressions for *C. whitei* ($F_{1,28} = 9.27$, $P = 0.005$) and *C. dalmanni* ($F_{1,29} = 4.85$, $P = 0.036$) but not for *C. quinqueguttata* ($F_{1,23} = 0.46$, $P = 0.51$) contests. Inspection of Fig. 3 provides an explanation for this apparent contradiction. Once species mean effects are removed, *C. quinqueguttata* contest durations are comparable to those of the two dimorphic species over the same range of eye span differences, but the difference in eye span between *C. quinqueguttata* males is much less than in the two dimorphic species. The absence of a significant regression of encounter duration on eye span difference is consistent with eye span not being used for contest resolution in *C. quinqueguttata*.

In contrast to encounter duration, ANCOVA indicates that the number of aggressive encounters observed during a contest increased with age ($F_{1,77} = 14.5$,

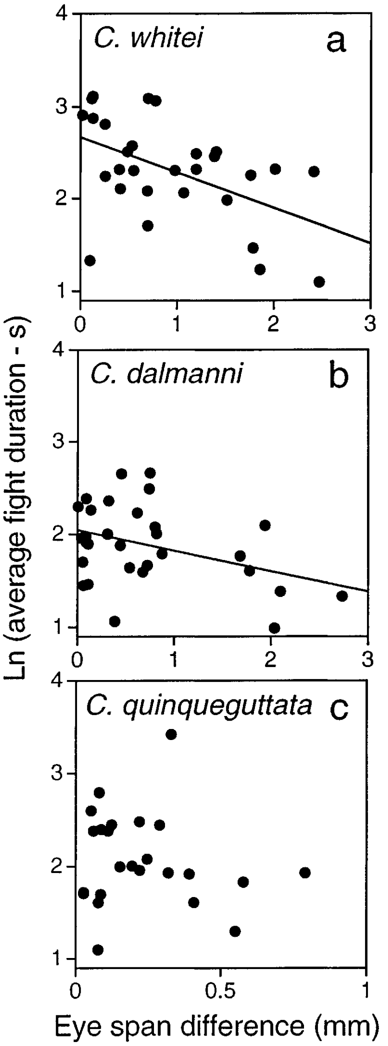

**Fig. 3** Duration of average aggressive encounter per 20-min contest plotted against the difference in eye span between the contestants for *C. whitei* (**a**), *C. dalmanni* (**b**), and *C. quinqueguttata* (**c**). Significant least-squares regression lines are shown

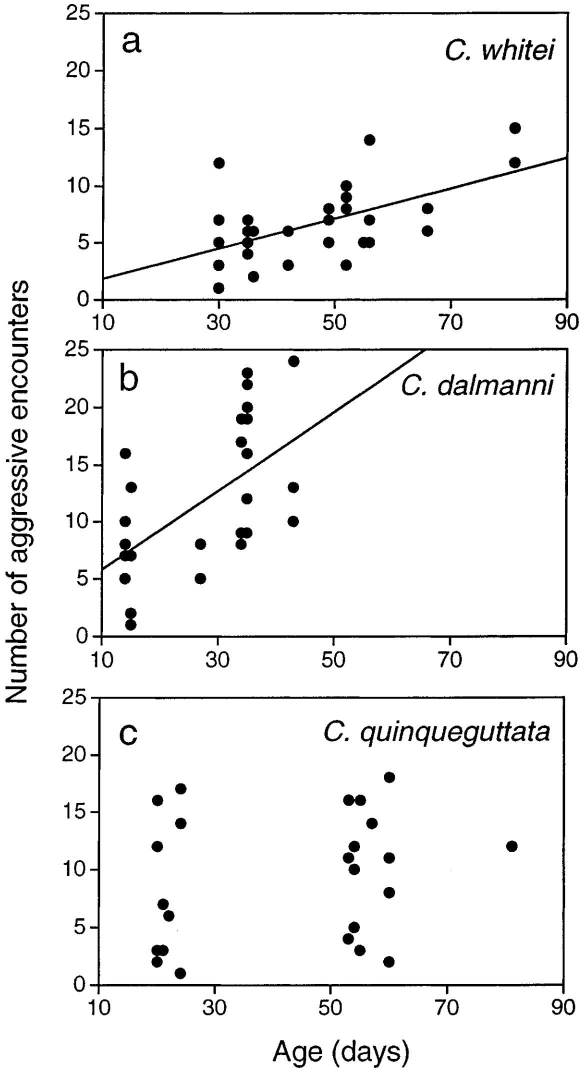

**Fig. 4** Number of aggressive encounters per 20-min contest regressed on the age in days since eclosion for each pair of contestants in *C. whitei* (**a**), *C. dalmanni* (**b**), and *C. quinqueguttata* (**c**). Significant least-squares regression lines are shown

$P = 0.0003$) and differed between species ($F_{2,77} = 12.1$, $P < 0.0001$), but was independent of eye span difference ($F_{1,77} = 0.26$, $P = 0.68$) and body length difference ($F_{1,77} = 0.61$, $P = 0.44$). A significant interaction between age and species ($F_{2,75} = 4.39$, $P = 0.01$) indicates that the slopes of the regressions between number of encounters on age differed between species (Fig. 4). The two sexually dimorphic species, but not the monomorphic species, exhibited significant positive regressions between number of encounters and age (*C. whitei*: $F_{1,27} = 12.78$, $P = 0.0013$; *C. dalmanni*: $F_{1,28} = 15.62$, $P = 0.0005$; *C. quinqueguttata*: $F_{1,22} = 0.99$, $P = 0.33$).

To determine if artificial selection modified fighting behavior, we compared average duration and number of aggressive encounters between outbred and selected-line *C. dalmanni* flies. We found no significant difference in log-transformed average encounter durations ($t = 1.72$, $P = 0.09$) or in the number of encounters ($t = 1.24$, $P = 0.22$) between outbred and selected-line flies.

## Discussion

Three types of evidence presented here indicate that males from the sexually dimorphic species assess eye span to resolve contests. First, eye span was a better predictor of fight outcome than any other measure of body size for both *C. whitei* and *C. dalmanni* males. Second, residual eye span was a highly significant predictor of fight outcome in contests involving *C. dalmanni* males from lines in which eye span had been altered experimentally by artificial selection. Third, the duration of a fight increased when the difference in the degree of eye span between opponents decreased, as predicted by game theoretic models of assessment (Enquist and Leimar 1983). By contrast, in the sexually monomorphic species, neither eye span nor any other size-related trait influenced fight outcome and fight duration did not depend on the degree of difference in eye span between opponents. Thus, eye span does not function to resolve contests in *C. quinqueguttata*. Taken together with studies showing that females from the dimorphic, but not monomorphic, *Cyrtodiopsis* species prefer to mate with males possessing larger eye span (Wilkinson et al. 1998a), these results indicate that eye stalks are likely to have influenced contest outcome and mate choice in a sexually dimorphic ancestor to *C. whitei* and *C. dalmanni* but not the sexually monomorphic ancestor common to all three species. Whether eye stalk elongation initially occurred in response to male competition, female choice, or simultaneously to both selective processes cannot be determined from these results. However, elongated eye stalks have evolved independently at least five times in diopsids (Wilkinson and Dodson 1997; R. Baker, R. DeSalle, G. Wilkinson, unpublished data). Thus, comparable mate choice and contest outcome studies utilizing other species groups from this family of flies can be conducted to resolve this issue.

The evolutionary transition from sexual monomorphism to dimorphism of eye span allometry almost certainly had an ecological basis. The two dimorphic species show many ecological similarities. Both exhibit a resource-defense mating system in which males compete with conspecifics to gain access to females at nocturnal aggregation sites on root threads (Burkhardt and de la Motte 1983, 1987; Wilkinson and Dodson 1997). Successful *C. whitei* males have been observed mating with over 20 females during a 30-min period after dawn (Lorch et al. 1993). Similar, albeit smaller, mating aggregations occur in *C. dalmanni* (Wilkinson and Reillo 1994). Aggregations have been reported primarily in sexually dimorphic species of stalk-eyed flies that inhabit riparian habitat in high densities (Burkhardt and de la Motte 1985; Wilkinson and Dodson 1997) and may represent a mechanism for detecting and avoiding nocturnal predators, such as ants. Whatever their function, once mating becomes associated with aggregations, selection should favor males that utilize honest signals to assess opponent size rapidly, thereby decreasing time and energy spent in fighting and increasing time spent in mating (Burkhardt and de la Motte 1987; Wilkinson and Dodson 1997). In contrast, the sexually monomorphic congener may have little need to advertise size or fighting ability. Observations in peninsular Malaysia indicate that *C. quinqueguttata* occurs at low densities and has never been found to form aggregations during the day or night (G.S. Wilkinson, personal observation). Mating has been observed to occur throughout the day (Kotrba 1996; G.S. Wilkinson, personal observation). Thus, intraspecific contests occur rarely. In this situation, contest resolution may be more efficiently mediated by the individual with the highest motivation (see below) rather than the largest body size.

To function effectively in contest resolution, eye span must accurately and reliably signal size and fighting ability. Accuracy of size assessment is enhanced by direct frontal comparison of eye stalks (McAlpine 1979) and by positive allometry between eye span and body size (Burkhardt and de la Motte 1987; Wilkinson and Dodson 1997). By orienting their eye stalks in parallel, competing males place their eye bulbs directly in front of the ommatidial region with highest visual acuity (Burkhardt and de la Motte 1983). Assuming that the resolution of the visual system does not decrease as eye span increases, a steeper regression between eye span and body size should enable a fly to assess opponent body size more accurately. The reliability of this signal, i.e., whether eye span correlates highly with body size (Eberhard et al. 1998), is probably high for two reasons. First, eye span of an adult fly cannot change once the exoskeleton hardens. Consequently, the correlation between eye span and body length will be higher, for example, than between eye span and body mass, because mass can change after eclosion. Second, development of an unusually large eye span for a particular body size seems likely to be costly (Nijhout and Emlen 1998). During metamorphosis, each larva has a fixed pool of resources to allocate between somatic tissue and eye stalks. A fly which allocated a disproportionate amount of resources to eye span would presumably be less able to survive and reproduce.

The degree of sexual dimorphism found in any population of stalk-eyed flies is likely, therefore, to result from a balance between selection acting against further eye span exaggeration and both intra- and intersexual selection for increased eye span. Artificial selection on relative eye span shows that the alternative explanation, that genetic variation for eye span allometry is absent, is not tenable. After ten generations of artificial selection on males, the slope of the regression of eye span on body length diverged (Wilkinson 1993). A similar response to selection on allometry has been reported for a horned beetle (Emlen 1996).

Eye span was a significant, but not perfect, predictor of fight outcome and duration for both sexually dimorphic species. Presumably, in those fights won by smaller-eye-span males, males either made errors in assessing opponent body size, or other factors influenced fight outcome. If assessment error occurs, then by the arguments described above, we expect fewer assessment mistakes in the species with greatest sexual dimorphism. Consistent with this prediction, *C. whitei* as the most sexually dimorphic species (Wilkinson and Dodson 1997) had the fewest contests in which eye span failed to predict fight outcome. However, the magnitude of the difference in eye span between opponents in some of the cases where smaller-eye-span individuals won fights suggests that other factors are also involved. One possibility is that males differed in current motivation. Because mass was not a better predictor of fight outcome than eye span, we doubt if males differed in recent feeding history prior to isolation. However, it is possible that males differed in lean body mass for either heritable or environmental reasons. This idea could be examined by comparing dry mass of competitors after a contest. Alternatively, individuals might differ in recent fighting history. While we did not use any male in more than one contest, we did house males in group cages prior to the experiment. In these cages, fights occurred regularly over access to food. Other studies on insects (Hack 1997) have indicated that a history of either success or failure can influence an individual's willingness to fight and fighting ability. The possibility that prior experience influences fighting ability is consistent with the increase in number of aggressive encounters with age for both sexually dimorphic species in this study, and with older male *C. dalmanni* being captured more often in aggregations in the field (Wilkinson and Reillo 1994). Further study is warranted to determine the importance of prior fighting on fight outcomes and durations in stalk-eyed flies.

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