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Aerial performance of stalk-eyed flies that differ in eye span

Abstract Stalk-eyed flies have eyes placed laterally away from the head on elongated peduncles. The elongation of eye span may increase the energetic cost of flight, reduce flight performance via aerodynamic effects or via increased load, or necessitate compensatory changes in other body dimensions. Body mass and body dimensions were measured to test the hypothesis that elongation of eye span is correlated with increased head mass in two closely related species of stalk-eyed flies. *Cyrtodiopsis whitei* is sexually dimorphic, with the eye span of larger males exceeding body length. *Cyrtodiopsis quinqueguttata* is sexually monomorphic with eye span substantially less than body length. Although eye span was significantly longer in *C. whitei*, head mass did not differ between species after accounting for differences in body mass. *C. whitei* males had longer wings, heavier thoraxes, and lighter abdomens in relation to body mass than did female *C. whitei* or *C. quinqueguttata* of either sex. Three-dimensional tracking of flight paths showed that path velocity and the horizontal component of velocity did not differ according to species or sex, but the long-eyed *C. whitei* males showed reduced overall aerial performance by flying at shallower ascent angles and reduced vertical velocity. Although increased mass loading does not occur in *C. whitei* males, increased drag, aerodynamic effects from the wake of the eye stalks, and constrained visual processing are possible mechanisms which could cause their reduced performance.

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Introduction

Sexual selection often results in exaggeration of morphological and behavioral characters when individuals of a given sex, usually males, experience a mating advantage through the mechanisms of female choice or male competition. Almost all recent theoretical models assume that elaborate male secondary sexual characteristics are costly to produce and to maintain (e.g., Grafen 1990a, b; Pomiankowski et al. 1991; Iwasa and Pomiankowski 1995; Kirkpatrick 1996; Pomiankowski and Iwasa 1997); thus, the mating benefit accrued by possession of such traits (sexual selection) is eventually offset by other fitness costs (natural selection). Costs and tradeoffs associated with maintaining elaborate secondary structures during adult life stages are becoming increasingly well documented and can take many forms, ranging from increased predation risk to physiological and life history trade-offs (see Andersson 1994 for review).

Recently, aerodynamic adaptations for flight and their association with ecological and social factors has received considerable attention (Evans and Thomas 1992; Thomas 1993; Møller et al. 1998; Barbosa and Møller 1999). Comparative studies of bird (e.g., Andersson and Norberg 1981; Balmford et al. 1994; Norberg 1995; Fitzpatrick 1999) and butterfly (e.g., Marden and Chai 1991; Wickman 1992) morphology suggest that both natural selection and sexual selection are important determinants of flight design. However, energetic and/or performance costs of carrying elaborate morphological traits have been difficult to document directly. In birds, reduced flight performance associated with elaborate plumage traits has mainly been inferred indirectly (but see Swaddle 1997), such as from measures of reduced foraging efficiency (e.g., Møller 1989; Møller et al. 1995a; Matyjasiak et al. 1999) or reduced survival (e.g., Møller and de Lope 1994).

Stalk-eyed flies (*Diptera*; *Diopsidea*) are emerging as an important model system for understanding how choosy females drive the evolution of showy male traits (e.g., Burkhardt and de la Motte 1988; Wilkinson et al. 1998b). In sexually dimorphic species of stalk-eyed flies, such as *Cyrtodiopsis whitei*, male mating success is correlated with eye span (Burkhardt et al. 1994; Wilkinson and Reillo 1994). Eyestalk length is heritable (Wilkinson and Taper 1999) and, thus, capable of responding to selection (Wilkinson 1993). Females show a preference for males with longer eye spans (Wilkinson et al. 1998a). In addition, males compete for access to and control of prime breeding sites (dangling rootlets under overhanging embankments) and for groups of females by comparing eye span and sometimes, if males are similar in size, in pitched battles (Lorch et al. 1993; Panhuis and Wilkinson 1999). Such observations indicate that eye span is under current sexual selection.

Sexual dimorphism in eye stalk length has arisen several times in the family Diopsidae (Baker et al., submitted). Variation between species and between sexes can be quite dramatic, as variation in eye span between closely related species can be more than ten-fold (Wilkinson and Dodson 1997). Physiological constraints generated by the elongation of eye stalks could create selectively important variation in flight performance and thereby limit further elaboration of the trait. Potential mechanisms include increased load (Marden 1987), increased aerodynamic drag, aerodynamic effects of the wake of the eye stalks in the stroke path of the wings, or increased difficulty integrating visual information (Buschbeck and Hoy 1998). Selectively important effects could be manifested directly as an increased energetic cost of flying and/or reduced flight performance, or by compensatory changes such as an increase in the relative amount of flight muscle. Here we present data on body dimensions and free flight performance for each gender of two species of stalk-eyed fly that differ dramatically in eye span (Fig. 1).
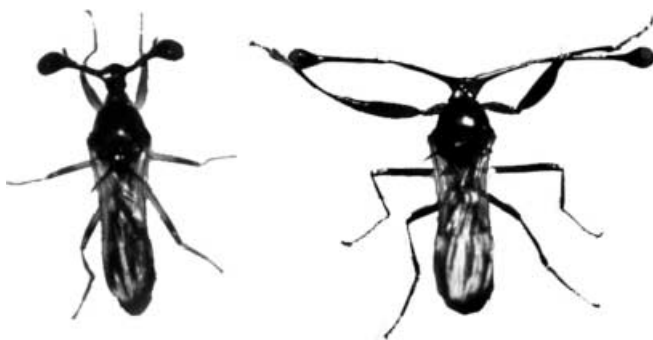

Fig. 1 Male stalk-eyed flies from the two species used in this study are shown here. *Cyrtodiopsis quinqueguttata* (*left*) are sexually monomorphic; females have similar eye spans. *Cyrtodiopsis whitei* (*right*) are sexually dimorphic; eye span of females is intermediate between male *C. whitei* and *C. quinqueguttata*

Materials and methods

Animal husbandry

The stalk-eyed flies used in this experiment were obtained from large stock populations of two species, *Cyrtodiopsis quinqueguttata* and *Cyrtodiopsis whitei* (Fig. 1), that are currently maintained at the University of Maryland at College Park in 40 × 40 × 120 cm Plexiglas population cages. Each cage was lined with moist blotting paper and cotton and kept in a temperature-controlled room at 25 °C with a 12 h light-dark cycle. Flies of both species were maintained on pureed corn media. See Lorch et al. (1993) for a more detailed description of laboratory methods. Progenitors of each population were netted in forested ravines 20–30 miles north of Kuala Lumpur, Malaysia, in January, 1989 and 1996. Directly prior to this experiment, flies of each species were housed in same sex groups of 15–30 individuals in small plastic cages (10 × 10 × 15 cm) lined with moist blotting paper and cotton and transported to Pennsylvania State University.

Morphological measurements

Using CO_2 anesthesia, ten flies of each species and sex combination were placed on their orbital and thoracic spines. A ×56 video image was digitized into a Macintosh computer, which provides a resolution of 50 pixels/mm. Eye span was measured from the outer edge of the ommatidia, body length from face to wing tip, wing length from the point of insertion to wing tip, and thorax width from the widest point on each animal (Wilkinson 1993). Each animal was then placed individually in a sealed 1.5 ml centrifuge tube and frozen at −20 °C. Within 48 h, all flies were weighed on a Mettler balance to the nearest 0.01 mg. After weighing, the head and abdomen were severed from the thorax, and the legs and wings were removed from the thorax. Each body section was then weighed separately.

Flight performance

Our aim in the present experiment was to obtain a direct measure of free flight to test the hypothesis that elaboration of eye stalks is accompanied by reduced flight performance. We utilized an apparatus modified for tracking individual free-flying insects in three-dimensional space (Marden et al. 1997; see below for details). Spatial coordinate data were then used to calculate mean and maximal flight velocities and angular trajectories for each gender of two species of stalk-eyed flies, *C. quinqueguttata* and *C. whitei*. Because *C. whitei* is sexually dimorphic for eye stalk length, females of this species serve as a control against the possibility of an interspecific difference that is unrelated to eye span.

Groups of flies were shaken from their home cages (15–30 individuals per cage; 15 *C. quinqueguttata* and 15 *C. whitei* females, 20 *C. quinqueguttata* males and 30 *C. whitei* males) into a temperature-controlled cabinet. Because most of the flies would not initiate flight voluntarily, individuals were stimulated to fly with light touch. Flights in still air were then tracked using the computerized motion-analysis system. The system consisted of two spatially calibrated CCD cameras with dedicated processors and software (MacReflex; Qualisys, Glastonbury, Conn., USA; http://www.qualisys.com). The tracking system was modified to detect dark objects (individual flies) against a light background. The back wall of the flight arena consisted of translucent white Plexiglas that was illuminated from behind by a 500 W incandescent light. The pixel coordinates of each fly were recorded 60 times per second and transformed into three-dimensional coordinates. Coordinates of a representative flight are shown in Fig. 2. Prior to measurement, the cameras were calibrated with a cube of known spatial coordinates. Calibration was then checked by computing the gravitational acceleration of a small clay sphere that was dropped through the calibrated airspace.
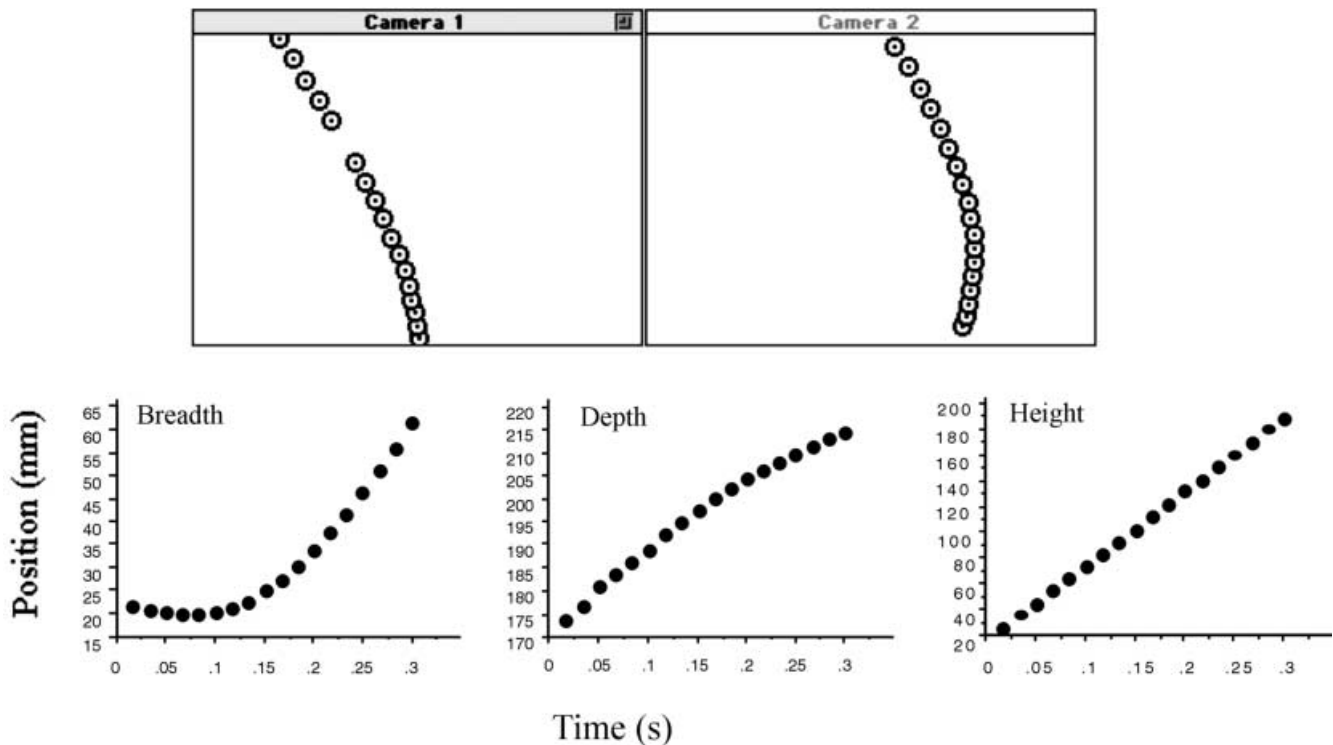
Fig. 2 Two-dimensional camera coordinates of a fly that was tracked at 60 samples per second (*top*). Units are pixels on a 19,500 × 27,000 array for each camera. Three-dimensional coordinates of a representative flight are shown at *bottom*. Note the fine resolution of motion. A rotating three-dimensional plot tracking data for fruit flies is available at http://cac.psu.edu/jhm10/project3.html

A cellophane tent of approximately 0.25 m × 0.25 m × 0.25 m bounded the airspace within the cabinet. For each flight trial, the computer recorded flights for a period of 6 min. A total of 28 trials were performed; 7 trials per species and sex combination. The same groups of individuals were used for each subsequent trial and, thus, some resampling may have occurred; 148 flights were successfully recorded and each flight is treated as an independent event in the statistical analyses. Air temperature within the test arena varied by a few degrees between trials (24.5–27 °C). Temperature was recorded and treated as a covariate in statistical analyses of flight performance.

Tracking data for each flight consisted of a single set of 4–41 (mean ± S.D. = 14 ± 8.3) three-dimensional spatial coordinates. Thus, each recorded flight segment averaged 0.23 s, which is ample time for small flies to attain steady-state aerodynamic conditions (Marden et al. 1997), particularly since all flights were recorded in midflight (i.e., not starting at 0 velocity). Horizontal, vertical, and the overall path velocity were determined from frame-to-frame changes in location. The framewise angular trajectory (0 is horizontal; 90 is vertical) was calculated as the inverse cosine of the ratio of horizontal velocity to resolved velocity.

Statistical analyses

Two-way analysis of variance (ANOVA) was used to test for differences in body mass and body length according to species and sex. Body mass was used as a covariate in all subsequent analyses of covariance (ANCOVA) for the morphological variables (i.e., head mass, thorax mass, abdomen mass, thorax width, eye span, and wing length). Statistical analyses of flight data were based on entire flights (both mean and maxima within a flight) rather than

framewise data. A similar ANCOVA was used to test for differences in flight performance between species and sex except that ambient temperature was used as a covariate instead of body mass.

Results

Morphological measurements

Unadjusted morphological data are presented in Fig. 3. Even though body length is similar between the two species, males and females of *C. whitei* are significantly lighter in body mass than *C. quinqueguttata* ($F_{1,36} = 83.00$, $P < 0.001$). Males of both species are significantly lighter than females ($F_{1,36} = 22.59$, $P < 0.001$). Mean values for all morphological traits adjusted for body mass differences between groups (least squares means from ANCOVA with body mass as a covariate) are presented in Table 1. All of the morphological traits measured were significantly related to body mass.

The eye span of *C. whitei* is significantly longer than that of *C. quinqueguttata* (Fig. 3B; Table 1). *C. whitei* is sexually dimorphic for eye span with males having larger eye spans than females. Eye span does not differ significantly between males and females of *C. quinqueguttata*, a species monomorphic with respect to eye span. However, two-way ANCOVA with body mass as a covariate indicates that mass of the head does not differ significantly between species or between sexes (Fig. 3A; Table 1).

Males and females of *C. whitei* have significantly longer wings relative to body mass than do *C. quinqueguttata* (Fig. 3B; Table 1). Males of both species have
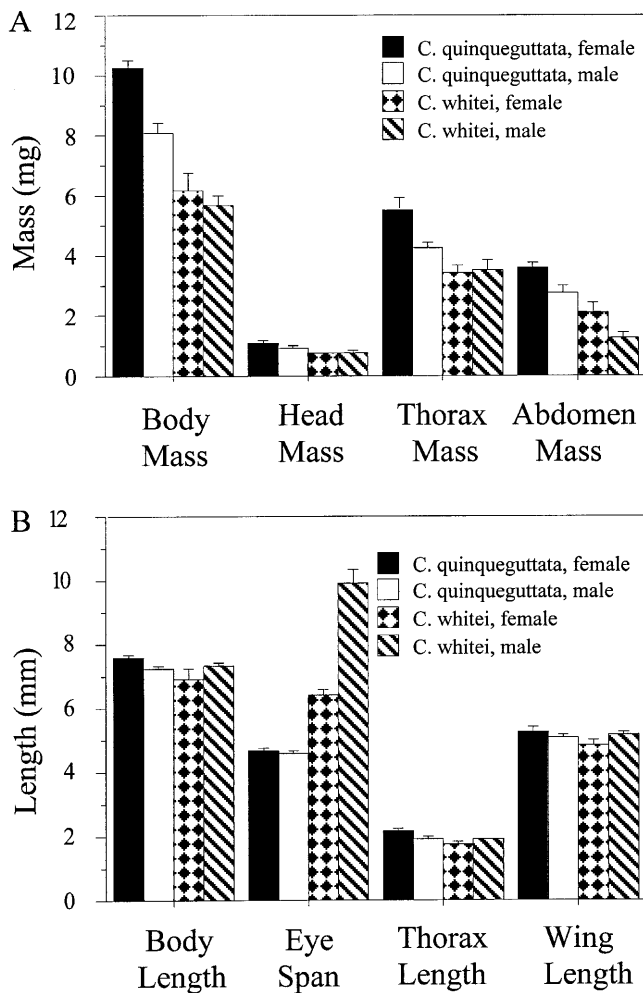
Fig. 3 Histograms of unadjusted means (± 1 S.E.) for body mass (A) and (B) body dimensions for 10 individuals measured from each species and sex combination. Note that same sex individuals of each species are paired next to each other

tion between species and sex. A *post hoc* orthogonal contrast indicates that wing length relative to body mass of male *C. whitei* is larger compared to wing length of the other three morphotypes (i.e., species/sex combinations; $P < 0.001$).

Thorax mass does not differ significantly between species or between sexes (Fig. 3A; Table 1). However, thorax mass does show a significant interaction between species and sex. A *post hoc* orthogonal contrast indicates that the thorax mass relative to body mass of male *C. whitei* is larger compared to the thorax mass of the other three morphotypes ($P = 0.007$). Data for flight muscle ratio (thorax mass/body mass) for each of the four species and sex combinations are presented in Table 2. Although neither species nor sex was statistically significant ($P > 0.05$), a *post hoc* orthogonal contrast indicates that *C. whitei* males have a significantly higher flight muscle ratio than the other three morphotypes ($P < 0.001$).

Abdomen mass does not differ significantly between species or between sexes (Fig. 3A; Table 1). However, as with thorax mass, abdomen mass shows a significant interaction between species and sex. In this case, a *post hoc* orthogonal contrast indicates that abdomen mass relative to body mass of male *C. whitei* is smaller compared to abdomen mass of all three other morphotypes ($P = 0.002$).

Flight performance

Mean values for all flight performance traits are presented in Figs. 4 and 5. For both the mean and maximal path velocity within each flight, there is a significant effect of sex but no interaction between species and sex (Table 3). Males of both species fly faster than females (Fig. 4).

Flight velocity can be partitioned into horizontal and vertical velocity. There are marginally significant species and sex interaction effects on mean ($P = 0.079$) and maximum ($P = 0.049$) horizontal velocity (Table 3). *C. quinqueguttata* males move more slowly horizontally than do *C. quinqueguttata* females, whereas *C. whitei*

significantly longer wings than females. The magnitude of the difference between males and females is somewhat larger in *C. whitei*, as indicated by a significant interac-

Table 1 Least squares means and ANCOVA results ($F_{1,35}$ values) for the effects of body mass, species (*C. quinqueguttata* versus *C. whitei*), and sex on a variety of morphological variables. LS Means values are controlled for body mass and presented with ± 1 standard error (S.E.)

Measurement	*C. quinqueguttata*		*C. whitei*		Species	Sex	Body mass	Species* Sex
	Female	Male	Female	Male				
Mass (mg)								
Head	0.79 ± 0.04	0.81 ± 0.02	0.80 ± 0.02	0.84 ± 0.03	0.2	1.6	60.6***	0.1
Thorax	4.02 ± 0.12	3.85 ± 0.07	3.72 ± 0.08	4.22 ± 0.10	0.1	3.1	164.0***	16.2***
Abdomen	2.34 ± 0.15	2.41 ± 0.09	2.63 ± 0.10	1.97 ± 0.12	0.2	6.7*	75.8***	13.2***
Dimensions (mm)								
Eye span	4.06 ± 0.25	4.40 ± 0.14	6.47 ± 0.17	9.80 ± 0.19	218.0***	98.1***	7.8**	85.4***
Thorax width	1.95 ± 0.06	1.89 ± 0.03	1.80 ± 0.04	1.90 ± 0.04	1.4	0.3	13.2***	4.7*
Wing length	4.92 ± 0.06	4.97 ± 0.04	4.97 ± 0.04	5.27 ± 0.05	7.5**	15.5***	41.2***	10.8**

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Table 2 Flight muscle ratio (thorax mass/body mass) for each of the four species and sex combinations are presented with ±1 standard error (S.E.). Although neither species nor sex was statistically significant ($P > 0.05$), a *post hoc* orthogonal contrast indicates that *C. whitei* males have a significantly higher flight muscle ratio than the other three morphotypes ($P < 0.001$)

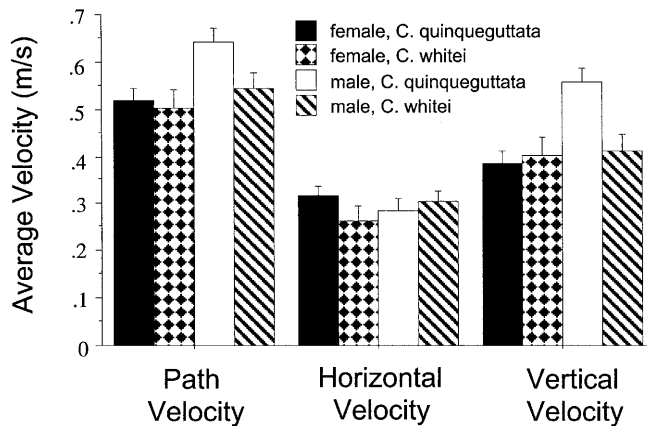| Species/sex	n	Thorax mass/body mass ±1 S.E.
C. quinqueguttata females	10	0.442 ± 0.005
C. whitei females	10	0.396 ± 0.016
C. quinqueguttata males	10	0.417 ± 0.007
C. whitei males	10	0.481 ± 0.008

Fig. 4 Histograms of unadjusted means (±1 S.E.) for path, horizontal and vertical velocity from each species and sex combination. A total of 148 flights were successfully recorded: 43 *C. quinqueguttata* females, 25 *C. whitei* females, 24 *C. quinqueguttata* males, and 56 *C. whitei* males
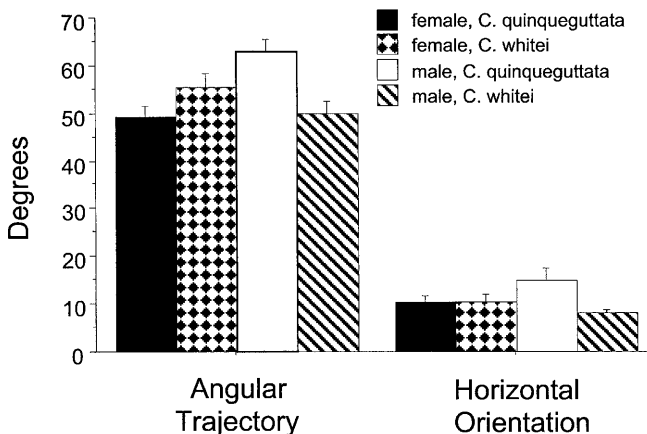

Fig. 5 Histograms of unadjusted means (±1 S.E.) for flight trajectory and flight orientation in the horizontal plane from each species and sex combination. A total of 148 flights were successfully recorded: 43 *C. quinqueguttata* females, 25 *C. whitei* females, 24 *C. quinqueguttata* males, and 56 *C. whitei* males

males move faster horizontally than do *C. whitei* females (Fig. 4).

Sex differences are evident for vertical velocity ($P = 0.001$ for mean; $P = 0.003$ for maxima), but the interaction between species and sex was not significant (Table 3). However, a *post hoc* orthogonal contrast indicates that *C. quinqueguttata* males fly at a significantly higher mean ($P = 0.007$) and maximum ($P = 0.014$) vertical velocity than the other three morphotypes (Fig. 4).

If *C. whitei* males move faster horizontally, but somewhat slower vertically, then we would predict a significant difference in the angular trajectory of flight paths. Indeed, this appears as a significant interaction between species and sex on mean angular trajectory ($P = 0.015$). The mean difference between the highest and lowest flight trajectory is greater than 10° (Table 3; Fig. 5). A *post hoc* orthogonal contrast shows that *C. quinqueguttata* males have the steepest flight trajectory ($P = 0.011$).

Finally, we found a significant species by sex interaction for variability in flight path orientation in the horizontal plane (measured as the log of the mean framewise change in horizontal angular trajectory), which is a measure of the straightness of the flight path ($P = 0.047$; Table 3; Fig. 5). *Post hoc* orthogonal contrasts showed that *C. whitei* males had the lowest value (i.e., flew along the straightest path; $P = 0.088$) and *C. quinqueguttata* males had the highest value ($P = 0.011$).

Discussion

Relative head mass does not differ between flies with different eye stalk lengths (Fig. 3). Although eyestalks are substantially longer in *Cyrtodiopsis whitei*, they are also thinner than the eye stalks of *Cyrtodiopsis quinqueguttata*. Thus we can reject the hypothesis of increased load (i.e., heavier eye stalks) as a potential cost leading to reduced flight performance. However, although *C. whitei* males do not show a reduction in overall flight velocity, their flight trajectory is more shallow and they do not ascend as rapidly. Therefore, elaboration of eyestalks is associated with a detectable reduction in flight performance.

Buschbeck and Hoy (1998) showed that displacement of the eye bulb away from the head in *C. quinqueguttata* is accompanied by dramatic changes in neural organization, including fewer but larger giant collector neurons. They suggest that the demand for rapid acquisition of visual information required for flight may be higher than can be handled by this neural arrangement, and thus might constrain flight performance. Indeed, stalk-eyed flies are relatively slow flying insects compared to other diptera. Our data do provide some evidence for this hypothesis. *C. whitei* males have the longest eye stalks and display the straightest flight paths, whereas *C. quinqueguttata* males showed greater maneuverability. This difference is consistent with slower or otherwise constrained visual processing in *C. whitei* males.

Alternatively, increased aerodynamic drag or disruption of airflow may be a mechanism causing reduced performance in *C. whitei* males. In the other species/sex

Table 3 ANCOVA results for the effects of temperature, species (*C. whitei* versus *C. quinqueguttata*), and sex on flight performance

Measurement	Species $F_{1,143}$	Sex $F_{1,143}$	Temperature $F_{1,143}$	Species* Sex $F_{1,143}$
Average				
Path velocity (m/s)	0.17	9.95**	5.19*	0.01
Horizontal velocity (m/s)	0.01	0.36	1.23	3.13
Vertical velocity (m/s)	0.31	10.82**	4.78*	1.39
Angular trajectory (degrees)	0.27	2.85	1.05	6.05*
Log flight orientation (degrees)	0.54	0.18	4.03*	3.56
Maximum				
Path velocity (m/s)	0.26	8.18**	4.50*	0.13
Horizontal velocity (m/s)	0.22	0.40	0.66	3.90*
Vertical velocity (m/s)	0.24	9.46**	5.15*	0.87
Angular trajectory (degrees)	0.21	0.97	0.05	3.75

$*P < 0.05; **P < 0.01$

combinations, the wings are substantially longer than an individual eye stalk (i.e., half eye span; Fig. 3B). Wingspan is greater than eye span. However, eyestalks of *C. whitei* males are slightly longer than their wings. Disruption of airflow by the eyes might negatively affect aerodynamic performance of the wings, which along with drag could explain the reduced angle of ascent observed for *C. whitei*.

It seems likely that the reduction in aerial performance seen in *C. whitei* males would be even more pronounced if not for the increase in relative wing length and flight muscle ratio. This result is to some degree expected because individuals that can reduce the negative impact of secondary sexual characters will be at a selective advantage. A similar result has been shown in the wing and tail morphology of barn swallows, whose central tail feathers and wings, wing span, wing area, wing loading, and aspect ratio, are all modified in males as compared to females (Møller et al. 1995b). Barn swallows with long tails have morphological modifications that presumably reduce the aerodynamic cost of the tail ornament.

In a fashion similar to what has been shown for male barn swallows, *C. whitei* males have longer wings, more massive thoraxes, and lighter abdomens in relation to their body mass than do female *C. whitei* or either sex of *C. quinqueguttata*. The thorax of holometabolous insects, such as stalk-eyed flies, is mainly flight muscle (Petersson 1995) and proportionally larger thoraxes provide a higher power margin (the ratio of power available to power required for weight support) and thus greater maximal performance (Marden 1987). Flight-muscle ratio (thorax mass/body mass; Table 2) is known to respond to selection for increased aerial performance, as shown by the covariation between body design and palatability/mimicry status in neotropical butterflies (Srygley and Chai 1990; Marden and Chai 1991), and the extraordinary hypertrophy of the flight musculature of territorial male dragonflies (Marden 1989). Increases in flight muscle ratio are accompanied by decreases in the relative mass of other body components, particularly the abdomen, thereby causing tradeoffs with other biological capacities that are not directly related to flight mechanics (i.e., ovarian mass and fecundity; energy reserves and starvation resistance). *C. whitei* flies show an increase in relative thorax mass and a decrease in abdomen mass (Table 1). In other insects these traits bring about an increase in aerial performance, yet *C. whitei* shows reduced vertical velocity and maneuverability. It appears that males of this species have a different body design that provides only partial compensation for the negative effect of long eye stalks on flight performance, and which may compromise other components of fitness, such as testes size (Presgraves et al. 1999) due to the reduced size of the abdomen.

The results presented here must be interpreted with some caution as they are based on a comparison of each gender from just two species (see Garland and Adolf 1994). However, the results of this experiment are consistent with our *a priori* hypothesis and with results of previous studies of factors that influence flight performance in a wide variety of organisms. A broader phylogenetic analysis is planned and would be required to rigorously test the generality of the relationship presented herein.

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