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Sexual dimorphism in wing beat frequency in relation to eye span in stalk-eyed flies (Diopsidae)

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Although male ornaments may provide benefits to individuals bearing them, such structures may also entail fitness costs. Selection should favour aspects of the phenotype that act to reduce such costs, yet such compensatory traits are often ignored in studies of sexual selection. If a male ornament increases predation risk via reduced locomotor performance, then there may be selection for changes in morphological traits to compensate for behavioural or biomechanical changes in how individuals use their morphology (or both). We took a comparative approach aiming to test whether changes in wing beat frequency are evolutionarily correlated with increases in male ornamentation across stalk-eyed fly species. Previous studies have shown that increased male eye span is evolutionarily correlated with increased wing size; thus, we tested whether there is additional compensation via increases in size-adjusted wing beat frequency. The results obtained revealed that relative wing beat frequency is negatively related to relative eye span in males, and sexual dimorphism in wing beat frequency is negatively related to dimorphism in eye span. These findings, in addition to our finding that eye span dimorphism is positively related to aspect ratio dimorphism, suggest that male stalk-eyed flies compensate primarily by increasing wing size and shape, which may then have resulted in the subsequent evolutionary reduction in wing beat frequency. Thus, exaggerated ornaments can result in evolutionary modifications in wing morphology, which in turn lead to adjustments in flapping kinematics, illustrating the tight envelope of trade-offs when compensating for exaggerated ornaments. © 2011 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2011, **104**, 670–679.

ADDITIONAL KEYWORDS: compensation – flight – locomotion – sexual selection.

INTRODUCTION

Although ornaments can provide benefits to males through increased mating success and a higher probability of winning an interaction with a rival male, ornaments may also impose costs upon the males bearing them (Andersson, 1994; Searcy & Nowicki, 2005). Indeed, it is the presence of such costs that may maintain reliability of ornaments (Zahavi, 1975; Grafen, 1990; Kotiaho, 2001). Nonetheless, male ornaments may increase predation risk by increasing conspicuousness (Endler, 1983; Husak *et al.*, 2006; Fowler-Finn & Hebets, 2010) or reducing locomotor performance during escape (Basolo & Alcaraz, 2003; Langerhans, Layman & DeWitt, 2005; Kruesi & Alcaraz, 2007; Oufiero & Garland, 2007). However, selection also acts on other traits to reduce potential costs of ornaments, resulting in the evolution of compensatory traits that may serve to reduce predation risk (Møller, 1996; Jennions, Møller & Petrie, 2001; Husak & Swallow, 2011). For example, potential flight performance costs of elongated tail feathers in birds appear to be offset by increased wing span and wing area when looking either within (Evans & Hatchwell, 1992; Evans & Thomas, 1992; Møller, de Lope & Saino, 1995) or across species (Andersson & Andersson, 1994; Balmford, Jones & Thomas, 1994). Increased predation risk in male ornamented *Schizocosa* spiders was

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*Corresponding author. Current address: Department of Biology, University of St Thomas, St Paul, MN, USA. E-mail: jerry.husak@stthomas.edu offset by altered escape behaviour compared to non-ornamented males (Fowler-Finn & Hebets, 2010; for other examples, see also Husak & Rouse, 2006 and Worthington & Swallow, 2010). Thus, to reduce the cost of increased predation risk, selection for compensation may result in changes to morphology (e.g. wing size) or in how morphology is used (e.g. escape behaviour).

Stalk-eyed flies have their eyes displaced laterally from the sides of their heads on stalks, the span of which can greatly exceed body length in the males of some species (Wilkinson & Dodson, 1997). The exaggerated eye span is a classic example of a male ornament that is favoured by female choice (Burkhardt & de la Motte, 1988; Wilkinson, Kahler & Baker, 1998; Hingle, Fowler & Pomiankowski, 2001; Cotton *et al*., 2006) and as a signal during male–male competition (Burkhardt & de la Motte, 1985; Panhuis & Wilkinson, 1999; Small *et al*., 2009; Egge, Brandt & Swallow, 2011). Despite the clear advantage that larger eye stalks can confer to males, the significantly increased moment of inertia of the head, caused by the exaggerated ornament in males compared to females (Ribak & Swallow, 2007), is predicted to decrease aerial turning performance of males. Flight performance trials, however, have not detected such a cost of the exaggerated eyestalks (Swallow, Wilkinson & Marden, 2000; Ribak & Swallow, 2007). Indeed, free-flying male *Teleopsis dalmanni* performed as well, or better, than females at aerial turning (Ribak & Swallow, 2007). One explanation for these counterintuitive results is that males have evolved mechanisms to compensate for the potential decrease in flight performance (Ribak *et al*., 2009; Husak *et al*., 2011). Consistent with this hypothesis, male stalk-eyed flies have larger thoracic masses (Swallow *et al*., 2000; Ribak & Swallow, 2007) and larger wings (Ribak *et al*., 2009; Husak *et al*., 2011) than females, and males with relatively longer eye stalks have relatively larger wings (Husak *et al*., 2011). Longer wings have a larger aerodynamic moment arm to potentially produce larger moments per wing beat than a shorter wing (Sotavalta, 1952; Ellington, 1984a). However, larger moments, which result from asymmetric force production during turns, should not provide any benefit during straight or hovering flight when symmetric wing strokes of the left and right wings create no net (overall) turning moment. Hence, the morphological compensation of sexually dimorphic male stalk-eyed flies poses an interesting question in trait evolution: what kinematic changes are associated with the development of a larger wing? Wing beat frequency scales negatively with wing length (Sotavalta, 1952) and hence it is expected that insects with larger wings should flap at lower frequency. However the dynamics of a flapping insect wing are quite complex and alternative adjustments can be made to keep aerodynamic power per wing beat constant via adjustments in wing beat amplitude, changes in the angle of attack of the wings, timing of wing rotation, and more.

We took a comparative approach aiming to test how male ornamentation affects wing beat frequency across species of stalk-eyed flies that differ in eye span and in the degree of eye span dimorphism. We predicted that increased relative eye span would result in decreased relative wing beat frequency as an indirect result of the morphological compensatory mechanism for the exaggerated ornament. Furthermore, we predicted that eye span dimorphism would be negatively related to dimorphism in wing beat frequency. Alternatively, it is possible that male flies have evolved altered kinematics so that they flap their larger wings at the same frequency as females or faster. This scenario may suggest a higher energetic cost and improved flight performance for flying in males. If this is the case, then one would predict a positive or no relationship between relative eye span and relative wing beat frequency or between eye span dimorphism and wing beat frequency dimorphism. To test these hypotheses, we measured wing beat frequency in 15 lineages of stalk-eyed files, and combined those data with morphological measures obtained from the literature to test whether male ornamentation influences wing kinematics.

MATERIAL AND METHODS

We collected species means for morphological variables and wing beat frequencies from a variety of sources. Morphological data are from Ribak *et al*. (2009) for all species, except the Brastagi and Brunei populations of *T. dalmanni*, *Teleopsis rubicunda*, *Teleopsis breviscopium*, and *Diasemopsis longipedunculata*. Morphological data for the latter species, and wing beat frequency data for all species were obtained from randomly drawn sexually mature flies in laboratory colonies at the University of Maryland (College Park, MD, USA). Eye span and wing morphology data for *D. longipedunculata* are from Baker & Wilkinson (2001) and from photographing and measuring wings of flies *sensu* Baker & Wilkinson (2003). For morphological measurements, flies were euthanized with CO_2, weighed on a microbalance, and photographed ventrally when lying on their backs (Wilkinson, 1993). Wings were removed at the hinge and photographed on a microscope slide (Baker & Wilkinson, 2001; Ribak *et al*., 2009). Morphological parameters measured were body mass, eye span (horizontal distance between distal sides of the two eyes), and wing length (the distance between wing tip and wing base, where the latter was defined at the first cross vein articulation). Wing length and wing area were calculated from planform digital images of the wings using a custom-written macro for SCION Image (Scion Corp.) (Ribak *et al*., 2009). Aspect ratio (AR) was calculated from wing area and wing length (R) by dividing the span ($2R$) of the two wings to the second power with the area of both wings (S): $\text{AR} = (2R)^2/S = 4R^2/S$ (Ellington, 1984a).

Wing beat frequency during hovering was measured using an optical tachometer (Unwin & Ellington, 1979; Unwin & Corbet, 1984) when the free-flying insect hovered between the tachometer and a light source. We placed one fly at a time in a $20 \times 15 \times 20$ cm (length × width × height) chamber that had the tachometer placed on the floor at the centre and a light source (12V DC Light projector, 1×10^6 Candela), hanging 30 cm from above. The upper roof of the chamber was covered with mosquito netting**.** The walls and floor of the chamber were made from white styrofoam, and air temperature within the chamber was maintained at 26° ± 1° during trials. A hot mirror (Edmund Optics) between the light source and the chamber was mounted at 45° to the light source to transmit only the visible light into the chamber while reflecting the longer wavelengths (heat) away. The flies were entered into the chamber and allowed to rest on one of the walls. When the fly was disturbed with a delicate brush, it took off and hovered towards the light at the centre of the chamber, which was above the tachometer. Trials lasted 10–20 s. The tachometer converted the light to an output voltage signal that included the frequency of flashing light reflected from the wings of the hovering insect. The voltage output signal was sampled (44.1 KHz) and converted to a digital audio file by the sound card of a desktop computer. We performed a spectral analysis on the audio signal using bioacoustics software (RAVEN, version 1.2.1; Cornell Lab of Ornithology) to extract the wing beat frequency of the insect (Hyatt & Maughan, 1994). Sample sizes and species means for males and females of each species are given in Table 1.

We first log-transformed data for all variables and performed analyses without consideration of phylogeny (i.e. 'tips' data). We tested for sex differences in wing beat frequency with analysis of covariance (ANCOVA), using body mass as the covariate and sex as the categorical variable. Because wing beat frequency and morphological variables often scale to body size, we regressed each variable (sexes separately) against body mass and obtained residuals for further analysis (see Supporting information, Table S1). We then used backwards stepwise multiple regression to determine the best predictor of residual wing beat frequency for males and females separately. Predictors entered into the initial model were residual eye span, residual wing length, and aspect ratio. We then divided the male mean of each variable by the corresponding female mean (neither log transformed) to obtain dimorphism values and examined Pearson product-moment correlations among dimorphism variables. We then used backwards stepwise regression to determine whether and how dimorphism in morphology (mass dimorphism, eye span dimorphism, wing length dimorphism, and aspect ratio dimorphism) predicted wing beat frequency dimorphism.

Table 1. Mean ± SE wing beat frequencies (Hz) for male and female stalk-eyed fly species used in the present study

	Males	Females
Diasemopsis aethiopica	160.5 ± 4.09 (4)	163.3 ± 6.74 (3)
Diasemopsis dubia	177.0 ± 1.00 (2)	168.0 ± 6.11 (3)
Diasemopsis longipedunculata	138.3 ± 1.60 (4)	154.0 ± 2.52 (3)
Diasemopsis meigenii	181.7 ± 5.24 (3)	196.8 ± 6.25 (4)
Diasemopsis signata	187.5 ± 11.5 (2)	184.3 ± 2.20 (6)
Diopsis apicalis	142.0 ± 1.53 (3)	142.5 ± 3.86 (4)
Teleopsis breviscopium	173.0 ± 12.5 (3)	205.3 ± 4.91 (3)
Teleopsis dalmanni – Brastagi	137.5 ± 3.28 (4)	164.5 ± 7.10 (4)
Teleopsis dalmanni – Brunei	165.3 ± 1.96 (7)	179.3 ± 2.16 (7)
Teleopsis dalmanni – Ulu Gombak	175.7 ± 3.67 (3)	188.7 ± 8.97 (3)
Teleopsis quinqueguttata	174.0 ± 4.00 (2)	170.0 ± 2.00 (3)
Teleopsis rubicunda	178.7 ± 0.67 (3)	195.7 ± 3.67 (3)
Teleopsis thaii	146.6 ± 9.30 (5)	182.2 ± 5.94 (5)
Teleopsis whitei	149.5 ± 1.71 (4)	166.5 ± 0.50 (2)
Sphyracephala beccarii	210.3 ± 5.02 (4)	213.8 ± 5.04 (4)

Common ancestry makes species means non-independent of each other (Felsenstein, 1985); thus, we also performed the same sets of analyses described above with phylogeny taken into account. Because there is no published phylogeny that includes all of the taxa we studied, we created a composite phylogeny (Fig. 1) from Baker & Wilkinson (2001), Wright *et al*. (2004), Swallow *et al*. (2005), and Földvári *et al*. (2007), and set branch lengths equal to 1 because the divergence times among the different species are unclear. We then used the PDAP:PDTREE module (Garland, Midford & Ives, 1999; Midford, Garland & Maddison, 2005) in MESQUITE, version 2.72 (Maddison & Maddison, 2009) to calculate standardized phylogenetically independent contrasts (Felsenstein, 1985).

RESULTS

Wing beat frequency scaled to body mass (Fig. 2A) for both males [mass$^{-0.17}$, $r^2 = 0.51$, $P = 0.003$; 95% confidence interval (CI) –0.07 to –0.27] and females (mass$^{-0.18}$, $r^2 = 0.41$, $P = 0.01$; 95% CI: –0.05 to –0.31). The slope of this relationship did not differ between the sexes (ANCOVA: $F_{1,26} < 0.001$, $P = 0.95$), although the intercept did (ANCOVA: $F_{1,27} = 5.06$,

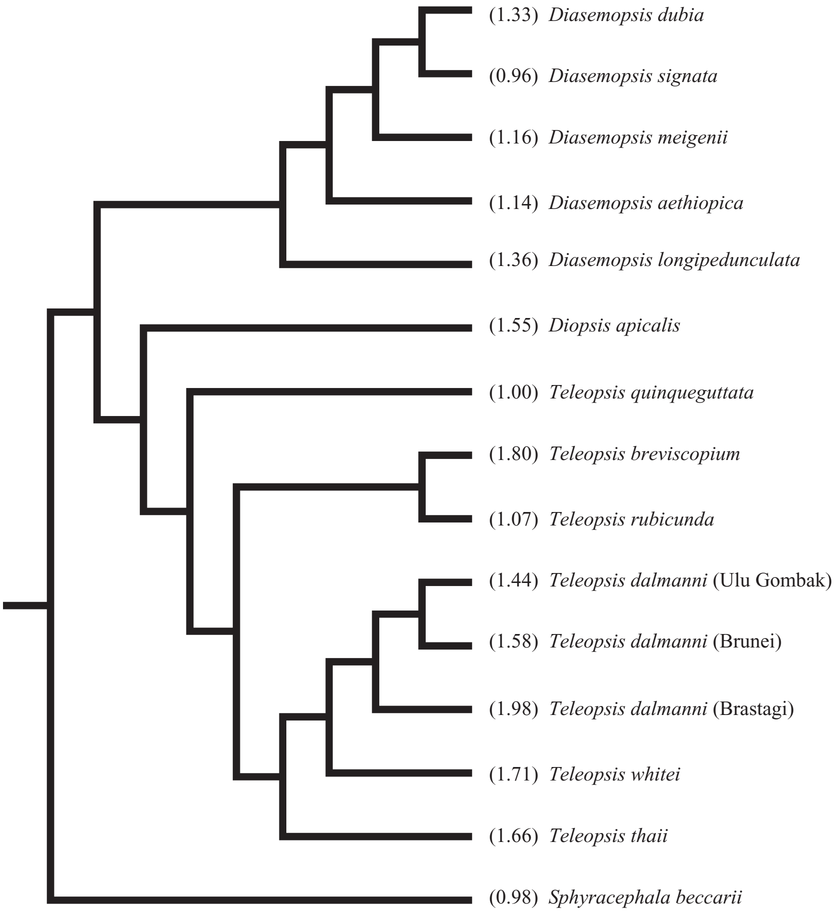

Figure 1. Phylogeny of the stalk-eyed fly species used in this study with eye span dimorphism index for each species in parentheses (mean male eye span divided by mean female eye span; for details, see text). The phylogeny is a composite phylogeny *sensu* Baker & Wilkinson (2001), Wright *et al.* (2004), Swallow *et al.* (2005), and Földvári *et al.* (2007), pruned to include only species in the present study. Branch lengths are not to scale.

$P = 0.03$). Analysis of independent contrasts revealed similar results (i.e. wing beat frequency scaled to body mass) (Fig. 2B) for both males (mass$^{-0.17}$, $r^2 = 0.46$, $P = 0.008$; 95% CI: –0.05 to –0.28) and females (mass$^{-0.15}$, $r^2 = 0.28$, $P = 0.05$; 95% CI: 0.001 to –0.31). However, note that, although the P-value was significant for females, the 95% CI includes zero. The relationship between independent contrasts of wing beat frequency and mass did not differ between the sexes in slope (ANCOVA: $F_{1,24} = 0.02$, $P = 0.89$) or intercept (ANCOVA: $F_{1,25} = 0.46$, $P = 0.50$).

Backward stepwise regression with residual eye span, residual wing length, and residual aspect ratio as independent variables revealed that residual wing length was the only significant (negative) predictor of residual wing beat frequency for females ($r^2 = 0.31$, $F_{1,13} = 5.74$, $P = 0.03$). For males, residual wing length was the only predictor that approached significance as a predictor of residual wing beat frequency ($r^2 = 0.23$, $F_{1,13} = 3.91$, $P = 0.07$). When analyzing independent contrasts for females, residual wing length was again the only significant (negative) predictor of residual wing beat frequency ($r^2 = 0.35$, $F_{1,12} = 6.49$, $P = 0.03$); however, for males, residual eye span became the only significant (negative) predictor ($r^2 = 0.30$, $F_{1,12} = 5.11$, $P = 0.04$).

Backward stepwise regression with mass dimorphism, eye span dimorphism, wing length dimorphism, and aspect ratio dimorphism as independent variables revealed that eye span dimorphism was the only significant predictor of wing beat frequency dimorphism ($r^2 = 0.52$, $F_{1,13} = 14.34$, $P = 0.002$; Fig. 3A, Table 2). The same results were found when analyzing independent contrasts ($r^2 = 0.51$, $F_{1,12} = 12.29$, $P = 0.004$; Fig. 3B, Table 2).

DISCUSSION

We found no evidence that wing beat frequency of males has increased in response to an evolutionary

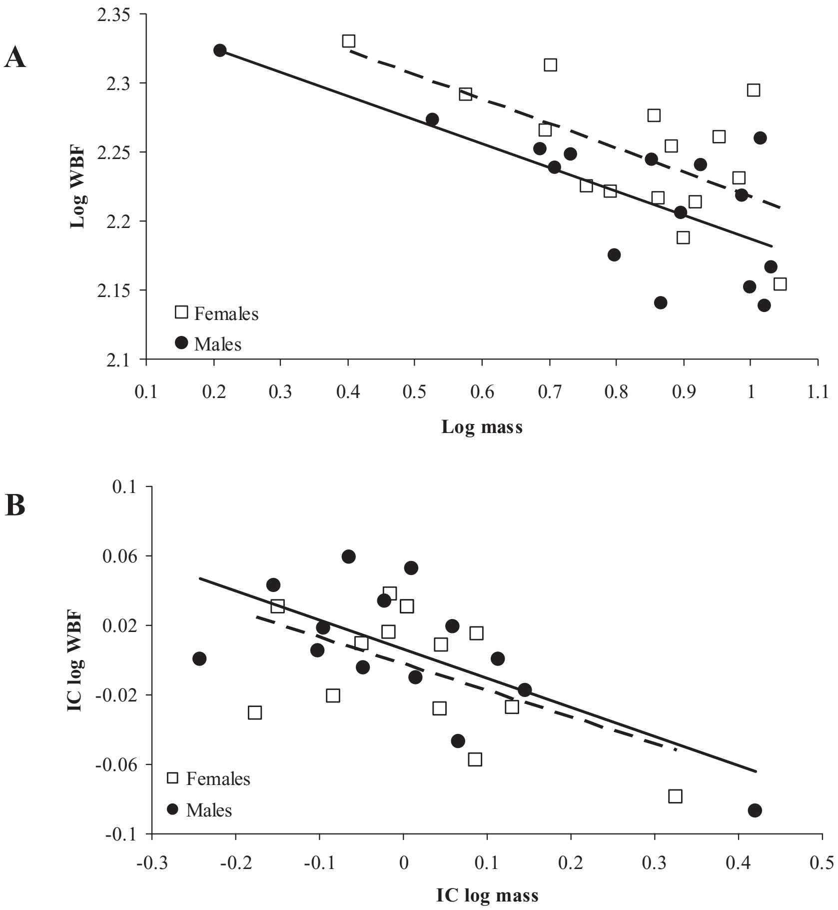

Figure 2. Allometry of wing beat frequency (WBF) for males (filled circles) and females (open boxes) across stalk-eyed fly species (Diopsidae) (A) not taking into account phylogeny and (B) taking phylogenetic relationships into account with independent contrasts (IC). Lines represent the best-fit least-squares regression lines for males (solid lines) and females (dashed lines).

Table 2. Correlation matrix of morphological and wing beat frequency dimorphism in stalk-eyed flies (Diopsidae) using species means Pearson correlation coefficients from analysis of 'tips' species means are above the diagonal, and correlation coefficients from analysis of phylogenetically independent contrasts are below the diagonal

	Body mass dimorphism	Eye span dimorphism	Aspect ratio dimorphism	Wing length dimorphism	Wing beat frequency dimorphism
Body mass dimorphism	–	0.66**	0.22	0.67**	–0.66**
Eye span dimorphism	0.31	–	0.47	0.76**	–0.77**
Aspect ratio dimorphism	0.25	0.60*	–	0.59*	–0.23
Wing length dimorphism	0.36	0.67**	0.49	–	–0.61*
Wing beat frequency dimorphism	–0.31	–0.71**	–0.36	–0.48	–

Statistical significance: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$. Sample sizes are given in parentheses.

increase in male eye stalk length. Indeed, we found the opposite: relative eye span of males had a negative relationship with relative wing beat frequency across species. Furthermore, wing beat frequency dimorphism was negatively related to eye span dimorphism. This means that as dimorphism in eye span becomes more male-biased across species, dimorphism in wing beat frequency becomes more

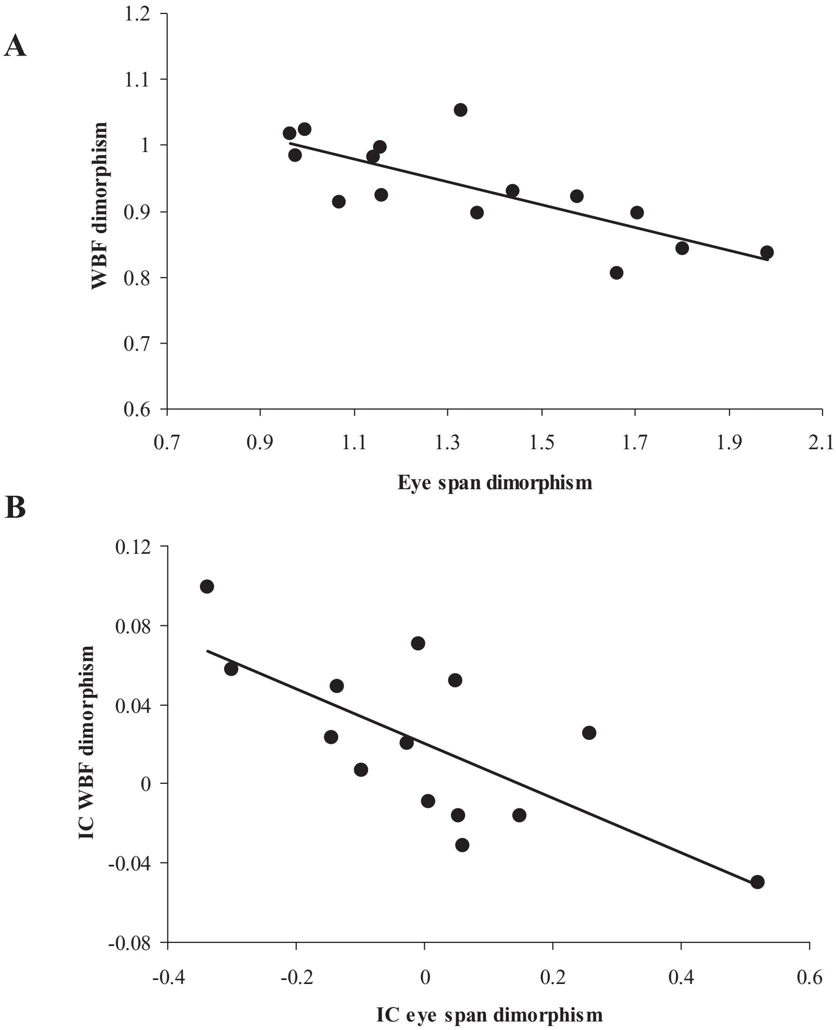

Figure 3. Relationship between wing beat frequency (WBF) dimorphism and eye span dimorphism across species of stalk-eyed flies (Diopsidae) (A) not taking into account phylogeny and (B) taking phylogenetic relationships into account with independent contrasts (IC).

female-biased. These results are consistent with the positive evolutionary relationship between wing size and eye span, as well as the positive evolutionary relationship between wing size dimorphism and eye span dimorphism (Ribak *et al.*, 2009). The findings obtained in the present study are also consistent with reported allometric studies of wing beat frequency among insects. Wing beat frequency across insect species scales with mass$^{-0.24}$ (95% CI: –0.18 to –0.29; Dudley, 2000), and the 95% CIs around our exponents across stalk-eyed fly species overlap substantially with this range. Thus, there does not appear to be deviation from the broader phylogenetic allometry of wing beat frequency for stalk-eyed flies due to ornamentation.

Compensation to enhance aerial performance can theoretically be made through the morphology and/or kinematics of flapping wings. The findings obtained in the present study suggest that wing size is the primary means of compensation for exaggerated ornamentation in stalk-eyed flies (Ribak *et al.*, 2009; Husak *et al.*, 2011), and that this morphological compensation in itself has resulted in kinematic changes: reduced wing beat frequency. The longer wings of dimorphic males (Ribak *et al.*, 2009; Husak *et al.*, 2011) are presumably needed to overcome the high moment of inertia of the body during aerial yaw turns (Ribak & Swallow, 2007). Indeed, a comparative study of rotational dynamics in flapping animals suggests that, proportionally, stalk-eyed flies may have the highest rotational inertia (for yaw turns) reported thus far in the animal flight literature (Hedrick, Cheng & Deng, 2009). Although the high moment of inertia of dimorphic males can limit aerial manoeuverability, it does not result in a mechanical handicap for straight flight or hovering. A male stalk-eyed fly with long eye stalks and a female with equal mass but short eye stalks would require the same mean aerodynamic force to hover. All else being equal, the aerodynamic force of a flapping wing approximately increases with wing length to the cubic power (Ellington, 1984c; see also below). Because males have evolved longer wings to produce larger torques during turning, in hovering, a male with reduced wing beat frequency would produce the same force as a female with equal body mass but shorter wings.

We can evaluate this idea by comparing the quasi-steady blade element model for flapping flight between males and females. In its most simplified form, the mean quasi-steady aerodynamic lift force, $\bar{F}$ of a wing flapping in harmonic motion within a horizontal stroke plane can be written as:

$$\bar{F} = 3.79 C_L R^2 S \Phi^2 n^2 \quad (1)$$

(*sensu* Ellington, 1999), where C_L is the aerodynamic lift force coefficient, R is the wing length, S is the wing area, Φ is the flapping amplitude and n is the flapping frequency (air density is included in the constant). This equation can be used to estimate the weight of the insect that can be supported in air during hovering. The simplified equation (for a more detailed variant of the model, see Ellington, 1984c) disregards the planform of the wing, but Ribak *et al.* (2009) showed that the nondimensional radius of the moment of wing area does not differ between males and females within species of stalk eyed flies. Thus, wing shape is not sexually dimorphic and we can disregard its effect in our subsequent discussion. When hovering, the mean aerodynamic lift force equals body weight, and, hence, the ratios that should hold are:

$$\frac{\bar{F}_{male}}{\bar{F}_{female}} = \frac{G_{male}}{G_{female}} = \frac{(C_L R^2 S \Phi^2 n^2)_{males}}{(C_L R^2 S \Phi^2 n^2)_{females}} \quad (2)$$

Where G is the weight of the fly. Rearranging gives:

$$\frac{G_{male}}{G_{female}}\left(\frac{n_{female}}{n_{male}}\right)^2 = \frac{S_{males}}{S_{females}}\left(\frac{R_{males}}{R_{females}}\right)^2\left(\frac{(C_L\Phi^2)_{males}}{(C_L\Phi^2)_{females}}\right) \quad (3)$$

In the present analysis, we have data for all parameters excluding the last term in brackets on the right. We can, therefore, statistically evaluate the biomechanical relationship between wing size and wing beat frequency. A slope of one in the linear relationship between $\frac{G_{male}}{G_{female}}\left(\frac{n_{female}}{n_{male}}\right)^2$ and $\frac{S_{males}}{S_{females}}\left(\frac{R_{males}}{R_{females}}\right)^2$ would imply that no further adjustment of the kinematics is required to explain the relationship between body mass, wing area, wing length, and wing beat frequency. Figure 4 shows such a relationship for our data ($F_{1,13} = 8.20$, $P = 0.013$), with 39% of the variation in one explained by the other ($r^2 = 0.39$). The 95% CI for the slope (0.17–1.19) includes one, which thus suggests that statistically $\left(\frac{(C_L\Phi^2)_{males}}{(C_L\Phi^2)_{females}}\right)$ for stalk-eyed flies is not different than 1.0. However, we note that the situation is more complex because variation in residuals at higher values of both indices increases (Fig. 4), and these points represent two recently-diverged populations

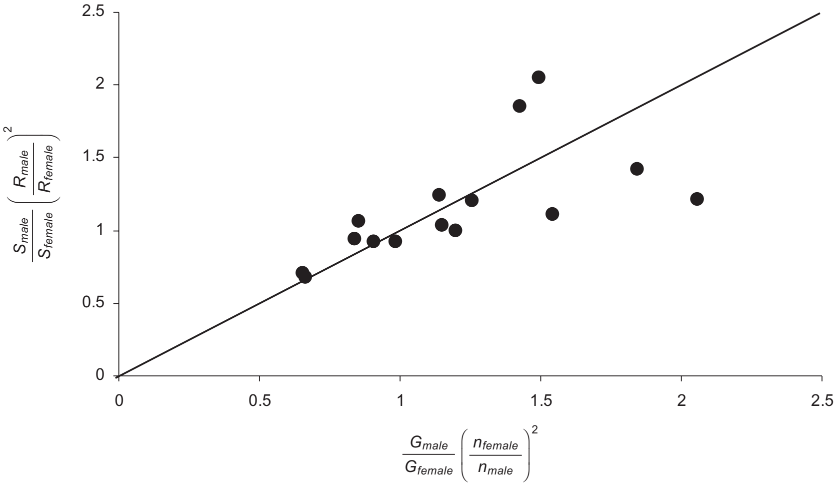

Figure 4. The linear relationship between the dynamic and morphological parameters of a highly simplified aerodynamic model of flapping flight (see text, Eqn 3). The diagonal line represents a slope of 1, from which our data did not significantly deviate (see text).

of *T. dalmanni* (Wright *et al*., 2004; Christianson, Swallow & Wilkinson, 2005; Swallow *et al*., 2005) and a species recently diverged from *T. dalmanni* (*Teleopsis thaii*; Földvári *et al*., 2007). It is possible that the recent evolutionary divergence in ornament allometry and other aspects of the phenotype have unpredictably affected this relationship. Future work aiming to elucidate this should focus on the higher and lower than expected wing beat frequency of these populations.

The present study reveals a potentially complex evolutionary influence of male ornamentation on wing kinematics. Numerous studies have investigated insect flight mechanics (Dudley, 2000), although little attention has been given to the potential impacts of male ornamentation on insect wing kinematics in free flight. The data obtained in the present study suggest that eye span has not directly influenced wing beat frequency over evolutionary time, although there is an indirect effect. Instead of males increasing wing beat frequency to mitigate reduced flight performance, males appear to compensate for increased eye span largely by increasing wing size (length and area; Ribak *et al*., 2009; Husak *et al*., 2011). The enlarged wings most likely then resulted in an evolutionary decrease in wing beat frequency because, in general, large wings have a lower wing beat frequency (Sotavalta, 1952; Dudley, 2000; Vigoreaux, 2006). Perhaps over evolutionary time, it is more efficient to modify wing development and architecture than to change the muscle properties that determine wing beat frequency, especially when compensation is required only for turning during flight. However, we only measured one aspect of wing kinematics, and it is possible that there are sex differences in other aspects of how wings are used during flight, such as burst flight speeds or differences in the stroke plane or amplitude (Ellington, 1984b; Dudley, 1995; Lehmann & Dickinson, 1997; Dudley, 2000; Sane, 2003; Dillon & Dudley, 2004; Roberts, Harrison & Dudley, 2004). The wide CIs found around the positive relationship shown in Figure 4 suggests that there may be further kinematic compensation that remains undetected. Future work along these lines will be very instructive for a better understanding of the morphological and performance consequences of ornaments.

We did not detect any effect of aspect ratio on wing beat frequency in either sex, and aspect ratio dimorphism was not significantly correlated with wing beat frequency dimorphism. However, we did find a positive evolutionary correlation between eye span dimorphism and aspect ratio dimorphism. The effect of aspect ratio is represented in Eqn 3 through the product of wing area and wing length (because $\mathrm{AR} = 4R^2/S$). A previous study of stalk-eyed flies also found a positive evolutionary correlation between aspect ratio dimorphism and eye span dimorphism, although the relationship lost significance when phylogeny was considered (Ribak *et al*., 2009). Our finding of a significant relationship, when using many of the same species, is very likely to be a result of the greater number of species in the present analysis. Thus, it appears that changes in wing aspect ratio may also be a compensatory mechanism for increasing eye span over evolutionary time because wings with higher aspect ratio have greater aerodynamic efficiency (Norberg, 1990; Frazier *et al*., 2008). To improve flight performance in cold environments, cold-reared *Drosophila* develop larger wings with higher aspect ratios compared to flies that develop in warmer environments (Frazier *et al*., 2008). Because small wings with low aspect ratio would generate insufficient aerodynamic forces at low wing beat frequencies (in a cold environment), large wings and greater aspect ratio may be an adaptation to aerodynamic constraints imposed upon the insect (Frazier *et al*., 2008). The finding in the present study of a correlation between wing length dimorphism and eye stalk dimorphism, as well as aspect ratio dimorphism and eye stalk dimorphism, is further evidence of compensation for the aerodynamic constraints to manoeuverability imposed by eye stalk length. Future comparative studies will reveal the generality of such morphological compensation to overcome aerodynamic constraints in flying insects.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Scaling of morphological and wing beat frequency data with body mass in stalk-eyed flies (Diopsidae) using species means without taking phylogeny into account and using phylogenetically independent contrasts (IC).