Compensation for exaggerated eye stalks in stalk-eyed flies (Diopsidae)

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Summary

1. Exaggerated male ornaments often are hypothesised to increase predation risk due to reduced locomotor performance, yet empirical evidence supporting this proposition is equivocal. In part, current costs of ornaments may be difficult to detect in nature due to the evolution of compensatory mechanisms that offset detrimental effects.

2. The exaggerated eye stalks of male stalk-eyed flies increase their moment of inertia compared with females, yet males do not suffer a flight performance decrement. We tested for evidence of compensation within seven species of stalk-eyed flies, examining eyespan and wing size in four dimorphic and three monomorphic species.

3. We found that, within species, males had larger wings than females in two species dimorphic for eyespan but not in any monomorphic species. In males of the dimorphic species, there were positive relationships between relative eyespan and relative wing area, indicating compensation, whereas there were no such relationships in females of the dimorphic species or in either males or females of the monomorphic species.

4. We propose that examining compensatory abilities relative to ornament size is a powerful way to test for costs of ornaments in correlational and experimental studies.

Key-words: compensatory traits, performance, ornament costs, wing shape

Introduction

Sexual selection is responsible for producing some of the most elaborate and bizarre traits known among animal taxa, including weapons and exaggerated ornaments used for rival assessment during male-male contests or for mate selection by the opposite sex (Andersson 1994; Emlen 2008). Such structures are thought to be reliable indicators of individual 'quality', with reliability of the indicator maintained via costs associated with the structure (Zahavi 1975; Grafen 1990; Pocklington & Dill 1995; Berglund, Bisazza & Pilastro 1996; Kotiaho 2001). The costs can be due to the response of the intended receiver (e.g. 'social control' hypotheses, Rohwer 1977; Hurd 1997) or to the development, use or maintenance of the structure (Maynard Smith & Harper 2003; Searcy & Nowicki 2005). One of the more intuitive expectations for exaggerated ornaments is that large structures will decrease locomotor performance of the individuals bearing them due to the physical burden of carrying them (reviewed in Oufiero & Garland 2007), yet

empirical evidence supporting this proposition is equivocal at best (Kotiaho 2001; Oufiero & Garland 2007). A classic example is the hypothesis that the elongated tail streamers of barn swallows (*Hirundo rustica*) increase drag during flight (Møller 1996; Møller *et al*. 1998), yet even this hypothesis has been controversial (e.g. Evans 1998; Buchanan & Evans 2000; Park, Rosén & Hedenström 2001). The exaggerated ornaments of male fishes have been shown to have performance costs for some species (Kruesi & Alcaraz 2007; Basolo & Alcaraz 2003; Langerhans, Layman & DeWitt 2005), but there is no detectable cost in other species (Ryan 1988; Nicoletto 1991). Male *Xiphophorus helleri* swordtail fish with longer swords were found to actually have greater escape performance (Royle, Metcalfe & Lindstrom 2006). One possible explanation for these contradictory findings is that there are other inter-correlated traits that obscure simple bivariate signal-performance relationships and costs that do exist (Oufiero & Garland 2007). This possibility has prompted more detailed studies that take into account the fact that selection does not act solely on the ornament independent of the remainder of the phenotype (e.g. Kirkpatrick 1987; Møller 1996; Jennions, Møller

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& Petrie 2001; Tomkins, Kotiaho & LeBas 2005). Since selection operates on the integrated phenotype, and not just single traits in isolation (Lande & Arnold 1983; Arnold 1983; Irschick *et al*. 2008), current costs of ornaments may be difficult to detect in a population due to past and current selection that has resulted in the evolution of compensatory mechanisms to deal with detrimental effects on performance and survival.

There are several examples of compensation for male ornaments via evolutionary changes in morphology related to flight performance. To apparently mitigate the aerodynamic costs of elongated tails used by male birds as ornaments, numerous species have evolved larger wings. Male barn swallows, for example, have greater wing spans, wing areas and aspect ratios and reduced wing loadings compared with females, and sexual dimorphism in tail length was positively correlated with dimorphism in wing length across populations (Møller, de Lope & Saino 1995a). Similar positive relationships between wing size and tail length have been found in long-tailed widowbirds (*Euplectes progne*, Craig 1989), Jackson's widowbird (*E. jacksoni*, Andersson 1992), and scarlet-tufted malachite sunbirds (*Nectarinia johnstoni*, Evans & Hatchwell 1992; Evans & Thomas 1992). For barn swallows (Møller, de Lope & López Caballero 1995b) and scarlet-tufted malachite sunbirds (Evans & Thomas 1992), experimental tail feather elongation of males resulted in increased foraging costs, suggesting that further elaboration beyond the ability to compensate may incur costs. Comparative studies across species of birds have shown that the sexual dimorphism in tail length is positively correlated with dimorphism in wing length (Andersson & Andersson 1994; Balmford, Jones & Thomas 1994), suggesting that males compensate for elaborate tail ornaments. Though most evidence for compensation comes from studies of birds, compensation for sexually selected traits has been proposed for other taxa. In the earwig *Forficula auricularia*, the positive relationship between relative elytra length (the modified, hardened forewing) and relative forceps size was suggested to be due to compensation for the burden of a sexually selected trait, the forceps (Tomkins, Kotiaho & LeBas 2005). Despite these examples, the role of compensatory traits in the evolution of ornaments, as well as whether compensatory traits impact our ability to detect costs of ornaments, remains unclear.

Stalk-eyed flies (Diopsidae) are characterised by having their eyes displaced laterally on long peduncles or stalks (Fig. 1). The family is composed of monomorphic species, where males and females do not differ in eyespan, and dimorphic species, where males have considerably larger eyespans than females, in some cases with an eyespan that exceeds body length (Wilkinson & Dodson 1997; Baker & Wilkinson 2001). The exaggerated eyespan in males of dimorphic species is under the influence of sexual selection via both female choice (Burkhardt & de la Motte 1988; Wilkinson, Kahler & Baker 1998; Hingle, Fowler & Pomiankowski 2001; Cotton *et al*. 2006) and male-male competition (Burkhardt & de la Motte 1985; Panhuis & Wilkinson 1999; Small *et al*. 2009). Eyespan of males in monomorphic species does not appear to be sexu-
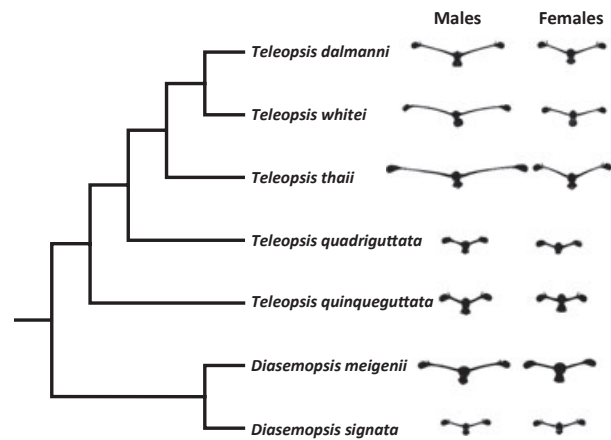

Fig. 1. Phylogenetic relationships among the species with representative pictures of male (left) and female (right) heads of dimorphic and monomorphic stalk-eyed flies. Tree is a composite phylogeny from Baker & Wilkinson (2001) and Földvári *et al.* (2007), pruned to include only species in this study. Branch lengths are arbitrary and not to scale.

ally selected (Wilkinson, Kahler & Baker 1998; Panhuis & Wilkinson 1999), and is likely closer to an optimum size shaped by natural selection, as is predicted for females of species with sex-limited ornaments (Lande 1980). However, in dimorphic stalk-eyed fly species, studies of eye stalk allometry suggest that females may also deviate from a biomechanically optimal head size (Baker & Wilkinson 2001), though females do not appear to experience sexual selection on eyespan (e.g. Al-Khairulla, Warburton & Knell 2003).

One consequence of the exaggerated eye stalks in dimorphic species is a large increase in the moment of inertia (for roll and yaw) of males compared with females (Ribak & Swallow 2007). As a result, males of dimorphic species require larger torques to rotate the body in air compared with females of equal size. Since the moment of inertia is an important determinant of flight manoeuverability (Dudley 2002; Fry, Sayaman & Dickinson 2003), males are predicted to suffer from decreased aerial manoeuverability. However, contrary to predictions, male *Teleopsis dalmanni* performed as well, or better, than females during free-flying turning behaviour (Ribak & Swallow 2007). This result is in general agreement with the finding that males of the dimorphic species, *T. whitei*, had only slightly, though significantly, lower vertical velocities compared with the monomorphic *T. quinqueguttata* (Swallow, Wilkinson & Marden 2000). Studies on stalk-eyed fly flight performance to date suggest that males appear to compensate for their biomechanical disadvantages with increased wing size, as well as thorax size – a proxy of flight musculature (Swallow, Wilkinson & Marden 2000; Ribak & Swallow 2007), though this hypothesis has not yet been specifically addressed. Confirming these studies of flight performance, staged laboratory interactions between flies and a predator revealed that females did not have higher survival than males when facing a predator; males in fact had higher survival (Worthington & Swallow 2010). Furthermore, a comparative analysis using species-mean values across 10 stalk-eyed fly

species revealed that sexual dimorphism in eyespan is positively correlated with dimorphism in wing size (Ribak *et al.* 2009), suggesting that changes in wing shape have co-evolved with changes in eyespan dimorphism over evolutionary time. Whereas the analysis by Ribak *et al.* (2009) revealed macro-evolutionary patterns of compensation across species, selection acts on the phenotype of the individual to shape the evolution of functional (wing size) and sexually selected (eyespan) traits. An intraspecific analysis is therefore critical to examine variation in compensation within a species or to allow predictions about the potential fitness consequences of that variation.

We tested for evidence of compensation within species of stalk-eyed flies, examining individual variation in, and covariation between, eyespan and wing morphology in four dimor-phic and three monomorphic species. We examined, within species, whether males and females differed in wing size, independent of body size, predicting wing dimorphism in species that are dimorphic for eyespan but not in species monomorphic for eyespan. To test for compensation via increased wing size, we examined relationships between relative ornament length and relative wing area. Since males of the monomorphic species have eyespans that are less than half the length of males of the dimorphic species (Wilkinson & Taper 1999; Ribak *et al.* 2009), we predicted compensation in males of dimorphic species but not in females or in either sex of monomorphic species. That is, we predicted positive relationships between relative eyespan and relative wing size in males of the dimorphic species, whereas we predicted no such relationships in females of the dimorphic species or in either
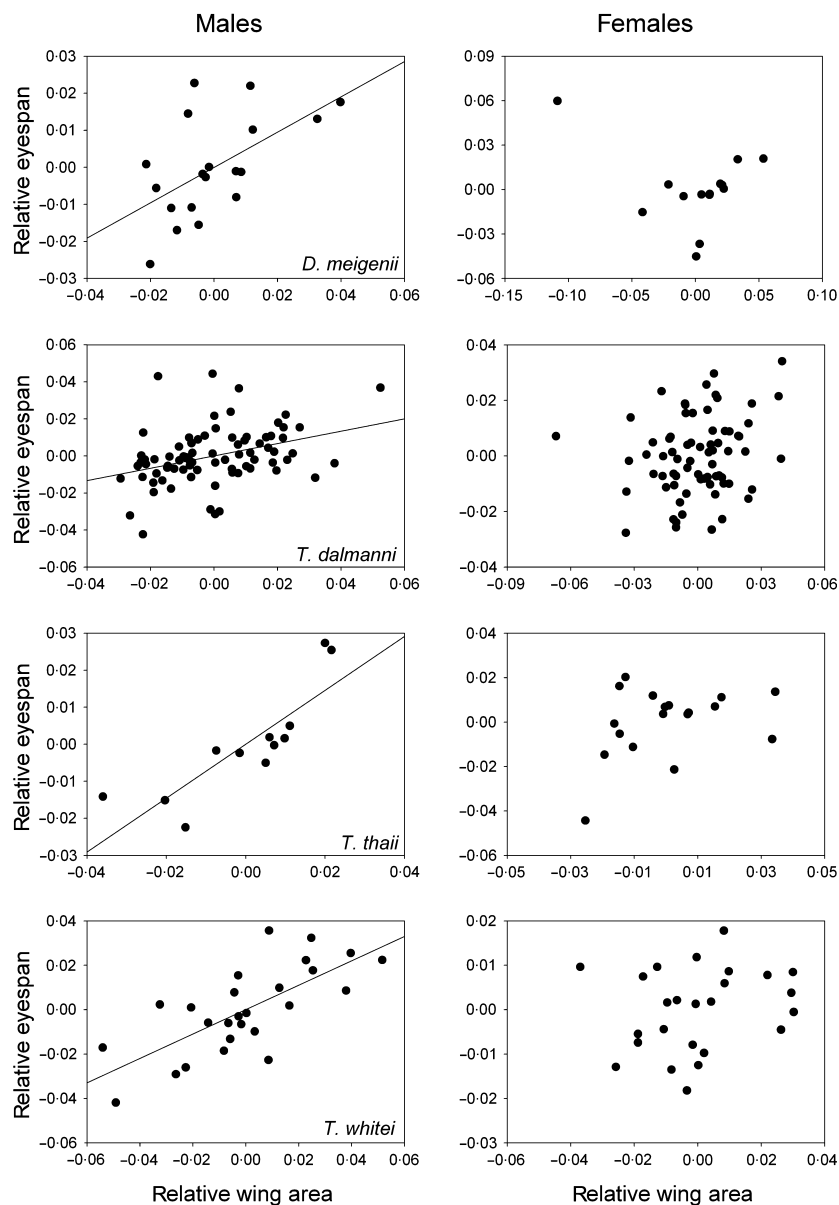

Fig. 2. Relationships between relative eyespan and relative wing area for males (left) and females (right) of four dimorphic species of stalk-eyed flies. Lines represent least-squares linear regression lines (where relationships were significant; see text) and are for illustrative purposes as in Fig. 4.

males or females of the monomorphic species. We also propose a novel way to test for relative costs of ornaments within a population by considering how far individuals deviate from the predicted average degree of compensation for their ornament size. Our approach will be most useful in species where manipulation of the ornament is difficult, such as in stalk-eyed flies, but it should be applicable to any species where compensatory traits have evolved to reduce ornament costs.

Materials and methods

STUDY SPECIES

We studied seven species of stalk-eyed flies: four dimorphic species (*T. dalmanni*, *T. whitei*, *T. thaii* and *Diasemopsis meigenii*) and three monomorphic species (*T. quinqueguttata*, *T. quadriguttata* and *D. signata*). The phylogeny for the species studied (Fig. 1) shows that monomorphism appears multiple times within Diopsidae (Wilkinson & Dodson 1997; Baker & Wilkinson 2001; Földvári *et al.* 2007). Individuals used in our analyses are a subset of those used in Wilkinson & Taper (1999) and Ribak *et al.* (2009), and we refer readers to those articles for details of laboratory housing of flies and specimen preparation. Briefly, flies were euthanised with CO_2 and photographed ventrally, after which wings were removed at the hinge for mounting on microscope slides. Flies were photographed while lying on their thoracic and orbital spines, a standard method (e.g. Wilkinson 1993) that yields highly repeatable body length measures ($< 1\%$ difference between two measures of the same individual on average). Wings of *T. dalmanni* ($n = 77$ males, $n = 71$ females), *T. quinqueguttata* ($n = 80$ males, $n = 79$ females) and *T. quadriguttata* ($n = 26$ males, $n = 24$ females) were permanently mounted on slides with Euporal (Bioquip, Gardena, CA, USA), following Baker & Wilkinson (2003) and photographed for digital analysis. Wings of *T. whitei* ($n = 26$ males, $n = 25$ females), *T. thaii* ($n = 12$ males, $n = 18$ females), *D. meigenii* ($n = 19$ males, $n = 14$ females) and *D. signata* ($n = 18$ males, $n = 13$ females) were not mounted in Euporal (because it was not necessary to archive wing data), but were covered with a microscope cover slip and photographed following Ribak *et al.* (2009). Individuals of *T. dalmanni*, *T. quinqueguttata* and *T. quadriguttata* used in our study were sampled from a larger quantitative genetic study of morphology (Wilkinson & Taper 1999) such that we did not analyse more than one offspring from each sire-dam pair. For the remaining four species, individuals were drawn at random from laboratory population cages (see Ribak *et al.* 2009). Thus, individuals were independent of each other for analysis.

MORPHOLOGICAL MEASUREMENTS

Body length was recorded as the distance from the anterior edge of the head to the posterior tip of the folded wings (Wilkinson 1993). This measurement, in our laboratory, has a tighter allometric relationship with eyespan ($r^2 > 0.8$) than when body length is measured to the tip of the abdomen ($r^2 < 0.6$; J.G. Swallow, unpublished data). Measuring body length to the tip of the abdomen is less reliable and repeatable because the abdomen of these flies often curls upwards and the abdomen changes in length with age as individuals accumulate fat (G.S. Wilkinson, unpublished data). Eyespan was measured as the distance between the outer edges of the ommatidia (Wilkinson 1993). We quantified wing area, which is a trait directly related to force production during flight (Ellington 1984) and is useful for extrapolating information about flight performance. We obtained measurements from the images using Scion Image (Scion Corp., Frederick, MD, USA) following Ribak *et al.* (2009), and we only briefly describe procedures below. We first oriented the wing images so that the long axis of the wing (e.g. wing length, the line connecting the base of the wing with the wing tip) was horizontal. The positions (2D coordinates) of points on the leading and trailing edges of the wing were determined at steps of five image pixels along the length of the wing and stored in a computer file. We obtained the coordinates using a custom-written macro programme for Scion Image (detailed in Fig. 2 of Ribak *et al.* 2009), which identified wing edges in the images and measured the positions and afforded objectivity and automation to the process. The wing edge position data were used to calculate area of the wing pair (from integrating the distances between wing edges along wing length and multiplying by two to account for both wings).

STATISTICAL ANALYSIS

Morphological variables were $\log_{10}$-transformed before analysis. We tested for sex differences for each species separately in wing area using ANCOVA with body length as a covariate. Since eyespan and wing area scaled to body size (Table S1 in the electronic Supporting information), we regressed each variable separately on body length to obtain residual values to test for relationships between relative eyespan and relative wing area. We also examined Pearson correlation coefficients to test for relationships between residual eyespan and residual wing area for each sex within each species. We repeated all analyses with wing length, and these results are presented as supplementary material (see Tables S2–S3 Supporting information).

Results

SEX DIFFERENCES IN WING MORPHOLOGY

For two of the four dimorphic species, *T. dalmanni* and *T. thaii*, ANCOVAs revealed that wing area was sexually dimorphic, with males having wings with greater area than females (Table 1). There was no difference between males and females in wing area for *D. meigenii* or *T. whitei* (Table 1). For all three monomorphic species, ANCOVAs revealed significant differences between males and females in wing area. However, for these species, females had larger wings than males (Table 1).

COMPENSATION

Residual wing area was positively correlated with residual eyespan in males of all dimorphic species (Table 2; Fig. 2). However, the two were not correlated for the females of any of the four dimorphic species. Similarly, there was no correlation between residual wing area and residual eyespan in males or females for any of the monomorphic species (Table 2; Fig. 3).

Discussion

Although exaggeration of ornaments is presumed to have an upper limit set by costs associated with bearing the ornament, correlated selection on compensatory traits may allow sexual

selection to maintain exaggeration or further exaggerate ornaments over evolutionary time (Møller, de Lope & Saino 1995a). Our analysis of wing morphology in seven species of stalk-eyed flies revealed that males of dimorphic species that had relatively larger eyespans also had relatively larger wings. In contrast, we found no such relationships for males of monomorphic species, where exaggerated eye stalks do not provide a mating advantage for males (Wilkinson, Kahler & Baker 1998; Panhuis & Wilkinson 1999). In addition, males of two eye-stalk dimorphic species had larger wings than females, whereas in all monomorphic species, females had larger wings than males. These findings are consistent with the hypothesis that natural selection favours traits in stalk-eyed flies that allow compensation for the detrimental locomotor effects of sexually selected ornaments. Alternatively, the positive relationships between residual eyespan and residual wing measures for dimorphic species could be due to direct sexual selection on wing size during aerial display, male-male competition, or female choice. However, this is unlikely given that flight does not seem important to display, wings are rarely displayed during fights (Egge, Brandt & Swallow in press), and males of monomorphic species appear to display the wings more than the dimorphic species studied (Burkhardt & de la Motte 1985; Panhuis & Wilkinson 1999).

Although most of our results matched our original predictions, some results were unexpected. For example, we found no sex difference in wing size for *T. whitei* and *D. meigenii*, yet compensation was evident within males of both species and within females of *T. whitei* (in wing length, see Table S3), but not within females in *D. meigenii*. A possible explanation for *T. whitei* is that females have longer wings to offset the costs of their enlarged eye stalks, which would also explain the significant relationship between relative eyespan and relative wing length for females of that species (Table S3). The reason is less clear for *D. meigenii*. One possible explanation is that there is selection for larger wings to compensate for increased eyespan in males, but there is also selection for increased wing size in females, perhaps to offset the costs of carrying eggs (see below). This is consistent with our finding that females of monomorphic species have relatively larger wings than males. In *D. meigenii*, it is possible that different selective pressures on male and female wings have resulted in equilibrium wing sizes for males and females that have a net effect of creating

wing monomorphism, despite dimorphism in eyespan. Alternatively, there may be unresolved intra-locus sexual conflict on wing size in *D. meigenii* (reviewed in Cox & Calsbeek 2009). Why we found this unexpected result in this species but not the others studied, and why selection on the sexes might be so dramatically different for *D. meigenii*, will require detailed studies of fecundity, body morphology and flight performance among species.

In all of the monomorphic species, females were found to have larger wings than males. While we can only speculate, it may be due to selection on females to overcome the burdens of flight with eggs. In other oviparous animals, reduced terrestrial locomotion in gravid females is a well-known 'cost' of reproduction (Shine 1980; Reznick 1985; Kullberg, Houston & Metcalfe 2002; Cox & Calsbeek 2010). If bearing eggs is costly to female flies, then compensatory mechanisms may be advantageous. Female *T. quinqueguttata* have greater thoracic masses (a proxy of flight muscle mass) than males (Swallow, Wilkinson & Marden 2000), supporting this hypothesis, but data on additional species are needed. Interestingly, female *T. dalmanni* with relatively longer eyespans have significantly more mature oocytes than females with relatively smaller eyespans (Cotton *et al.* 2010), and there may

Table 2. Correlations between relative eyespan and relative wing area in seven species of stalk-eyed flies

		r-value
Dimorphic species		
D. meigenii	Males	**0·57**
	Females	0·33
T. dalmanni	Males	**0·36**
	Females	0·21
T. thaii	Males	**0·84**
	Females	0·35
T. whitei	Males	**0·72**
	Females	0·21
Monomorphic species		
D. signata	Males	0·11
	Females	0·28
T. quadriguttata	Males	0·36
	Females	0·40
T. quinqueguttata	Males	0·18
	Females	0·21

Significant correlations ($P < 0.05$) are in bold.

Table 1. Results from ANCOVAS, showing tests for sexual dimorphism in wing area for seven species of stalk-eyed flies

	Body length*sex	Sex	Larger sex
Dimorphic species			
Diasemopsis meigenii	$F_{1,29} = 0.86, P = 0.36$	$F_{1,30} = 0.93, P = 0.34$	–
Teleopsis dalmanni	$F_{1,144} = 2.01, P = 0.16$	$F_{1,145} = 61.73, P < 0.001$	Males
T. thaii	$F_{1,26} = 0.10, P = 0.75$	$F_{1,27} = 15.57, P = 0.003$	Males
T. whitei	$F_{1,47} = 0.14, P = 0.71$	$F_{1,48} = 0.02, P = 0.90$	–
Monomorphic species			
D. signata	$F_{1,28} = 4.36, P = 0.046$	–	Females
T. quadriguttata	$F_{1,46} = 0.34, P = 0.56$	$F_{1,47} = 11.28, P = 0.002$	Females
T. quinqueguttata	$F_{1,155} = 1.02, P = 0.31$	$F_{1,156} = 5.65, P = 0.02$	Females

We did not test the main effect of sex for those with significantly heterogeneous slopes (i.e. a significant body length*sex interaction).
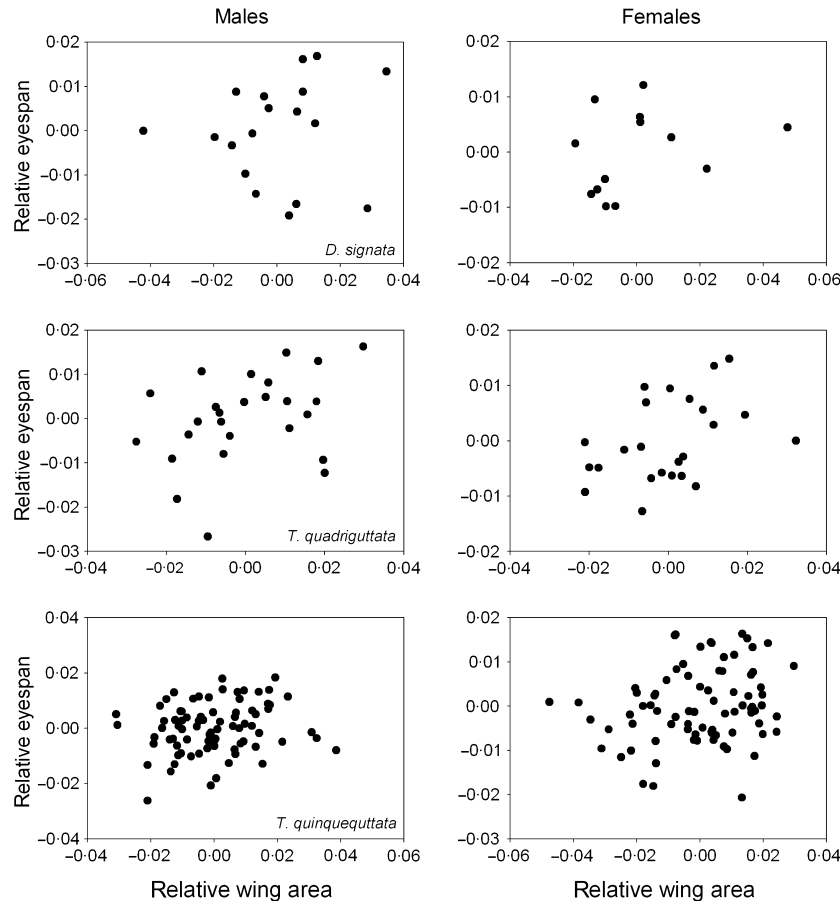
Fig. 3. Relationships between relative eyespan and relative wing area for males (left) and females (right) of three monomorphic species of stalk-eyed flies. None of the relationships was statistically significant.

be a scenario for selection to favour traits that reduce a reproductive burden. Both flight muscle mass and wing size contribute to force production during flight (Ellington 1984; Dudley 2000), so increased wing size may be a means of compensating. Thus, natural selection on wing size, and presumably flight musculature, in females of monomorphic species, combined with a lack of selection for male compensatory traits, due to an absence of exaggerated eye stalks, would result in female-biased dimorphism in wing size in monomorphic stalk-eyed fly species.

The significant relationships between relative eyespan and relative wing area in males of all four dimorphic species analysed indicate that, on average, individuals with larger ornaments have greater compensatory traits, but examination of those relationships (Fig. 2) reveals substantial variation. A linear regression line fit to the data represents average compensation within the population. Individuals that fall above this line have larger ornaments than their relative ability to compensate for them, whereas those below the line are 'over-compensating' for their relatively small ornament. Individuals that fall above the line with eye stalks that are relatively large for their relative compensatory ability are 'under-compensating' and are predicted to have performance or survival (i.e. viability) costs since they do not have the morphology to compensate for their relatively large ornament. On the other

hand, those below the line have eye stalks that are relatively small for their compensatory ability and are expected to have a viability advantage since they are 'over-compensating.' Thus, to test for costs of an ornament in a population, one would predict higher costs in those individuals above the line, with costs increasing, on average, as distance from the best-fit line increases (i.e. as relative compensatory ability decreases). However, fitness is also dependent on fecundity not just survival. Stalk-eyed flies with larger eyespans win more fights for access to females (Burkhardt & de la Motte 1985; Panhuis & Wilkinson 1999; Hingle, Fowler & Pomiankowski 2001; Small *et al.* 2009), and they are preferred more by females (Burkhardt & de la Motte 1988; Wilkinson, Kahler & Baker 1998; Cotton *et al.* 2006), but there is clearly a great amount of variation in male relative eyespan for all species (Figs 2 and 3). For any given wing size, those with relatively larger eyespans will have a fecundity advantage (Cotton *et al.* 2010), despite their performance or survival disadvantage, over those with smaller eyespans. Since fitness is a multiplicative function of viability and fecundity (Getty 1998, 2006), those with smaller relative eyespans but relatively larger wings are predicted to capitalise on their better survival to increase mating success over the duration of their longer lives. We note that this trade-off need not exist in all species, and whether it does depends on other life-history trade-offs (e.g. Lailvaux,
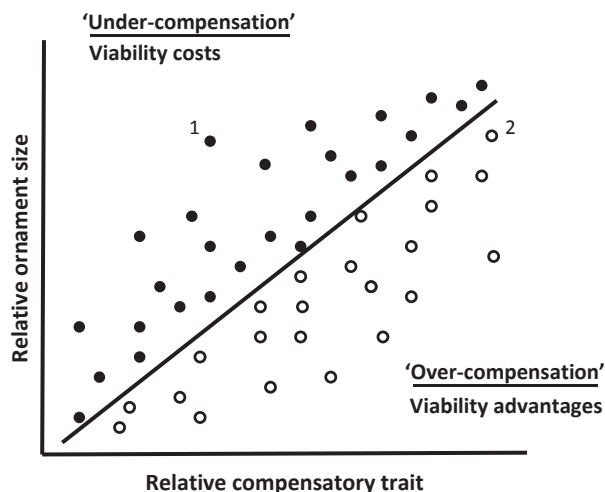
'Under-compensation'
Viability costs

Fig. 4. Conceptual illustration of compensation for exaggerated ornaments. By examining relationships between ornament size and compensatory traits, corrected for body size where appropriate, costs of ornaments may be revealed with more focused hypothesis tests. Individuals that fall above the regression line (filled, black circles; 'under-compensating') have ornaments that are larger than their predicted compensatory abilities and should have performance and/or survival (i.e. viability) costs. Individuals below the line (open circles; 'over-compensating') have greater compensatory traits than 'necessary' for their ornament size and should have performance and/or survival (i.e. viability) advantages. The line does not represent a theoretical or biomechanical optimum amount of compensation, but instead the average relative compensatory ability within a sex in a population from which one can derive hypotheses about relative costs. For example, the individuals represented by points one and two have similar relative eyespans, but individual one, with its relatively lower compensatory ability ('under-compensating'), is predicted to have higher costs than two ('over-compensating'). Nonlinear relationships may be possible, but the same predictions would apply. One could also examine multiple compensatory traits in multivariate space, such as with a principal components analysis that includes multiple morphological, physiological or performance traits. In such a multivariate analysis, the *x*-axis would be principal component scores or some other such composite variable. A multivariate approach could reveal important combinations of compensatory traits that form multiple 'solutions' to offset costs of exaggerated ornaments.

Hall & Brooks 2010; Lailvaux & Kasumovic 2011). At any given point along the *x*-axis, those above the line may have higher mating success at one point in time, but they should suffer lower survival overall, whereas those below the line could theoretically survive longer, during which time they could accumulate matings despite a lower probability of success at a given point in time. These hypotheses have yet to be tested, however.

Our analysis of compensatory traits in relation to ornamentation, however, is most explicit when considering performance or survival costs of ornaments, and can be useful when testing for the costs of ornaments and other sexual signals (Fig. 4). Our approach makes clear predictions about which individuals should have performance or survival costs (those 'under-compensating') and which should not (those 'over-compensating'). We point out that the regression lines in Figs 2–4 do not represent a biomechanical or physical 'optimum' compensatory ability, but instead average compensa-

tion for a sex within a population. Since the evolutionary significance of both fitness and fitness costs of an individual are important when considered relative to other individuals within a population, our approach allows a way to compare relative compensatory abilities within a population to determine which individuals should have higher costs and higher fitness. This approach is analogous to examining the fitness of individuals in 'morphological space' as has been done in numerous studies (Kingsolver *et al.* 2001; Blows 2007; Lailvaux, Hall & Brooks 2010). We note that our model is robust to situations where males are poorer performers (or survivors) than females on average in a population, because even in that situation, within males there are some males that are predicted to have higher costs (i.e. those 'under-compensating'). On the other hand, if one were to examine a sample of individuals from a population, testing for survival costs in relation only to ornament size, theoretically only half would display some degree of cost, whereas the other half would have a survival advantage. The net result would likely be no detectable relationship between ornament size and survival. Thus, future studies that seek to explore performance and fitness costs of ornaments and armaments should consider the potential for compensatory traits to obscure simple bivariate relationships between ornament size and performance.

Acknowledgements

References

Al-Khairulla, H., Warburton, D. & Knell, R.J. (2003) Do the eyestalks of female diopsid flies have a function in intrasexual aggressive encounters? *Journal of Insect Behavior*, **16**, 679–686.

Andersson, M. (1994) *Sexual Selection*. Princeton University Press, Princeton NJ.

Andersson, S. (1992) *Lek mating and sexual selection in Jackson's Widowbird (Euplectes jacksoni)*. PhD Dissertation, University of Göteborg, Göteborg, Sweden.

Andersson, S. & Andersson, M. (1994) Tail ornamentation, size dimorphism and wing length in the genus *Euplectes* (Ploceinae). *Auk*, **111**, 80–86.

Arnold, S.J. (1983) Morphology, performance, and fitness. *American Zoologist*, **23**, 347–361.

Baker, R.H. & Wilkinson, G.S. (2001) Phylogenetic analysis of eye stalk allometry and sexual dimorphism in stalk-eyed flies (Diopsidae). *Evolution*, **55**, 1373–1385.

Baker, R.H. & Wilkinson, G.S. (2003) Phylogenetic analysis of correlation structure in stalk-eyed flies (*Diasemopsis*, Diopsidae). *Evolution*, **57**, 87–103.

Balmford, A., Jones, I.L. & Thomas, A.L.R. (1994) How to compensate for costly sexually selected tails: the origin of sexually dimorphic wings in long-tailed birds. *Evolution*, **48**, 1062–1070.

Basolo, A.L. & Alcaraz, G. (2003) The turn of the sword: length increases male swimming costs in swordtails. *Proceedings of the Royal Society B*, **270**, 1631–1636.

Berglund, A., Bisazza, A. & Pilastro, A. (1996) Armaments and ornaments: an evolutionary explanation of traits of dual utility. *Biological Journal of the Linnean Society*, **58**, 385–399.

Blows, M. (2007) A tale of two matrices: multivariate approaches in evolutionary biology. *Journal of Evolutionary Biology*, **20**, 1–8.

Buchanan, K.L. & Evans, M.R. (2000) The effect of tail streamer length on aerodynamic performance in the barn swallow. *Behavioral Ecology*, **11**, 228–238.

Burkhardt, D. & de la Motte, I. (1985) Selective pressures, variability and sexual dimorphism in stalk-eyed flies (Diopsidae). *Naturwissenschaften*, **72**, 204–206.

Burkhardt, D. & de la Motte, I. (1988) Big 'antlers' are favored: female choice in stalk-eyed flies (Diptera, Insecta), field collected harems and laboratory experiments. *Journal of Comparative Physiology A*, **162**, 649–652.

Cotton, S., Fowler, K. & Pomiankowski, A. (2004) Condition dependence of sexual ornament size and variation in the stalk-eyed fly *Cyrtodiopsis dalmanni* (Diptera: Diopsidae). *Evolution*, **58**, 1038–1046.

Cotton, S., Rogers, D.W., Small, J., Pomiankowski, A. & Fowler, K. (2006) Variation in preference for a male ornament is positively associated with female eyespan in the stalk-eyed fly *Diasemopsis meigenii*. *Proceedings of the Royal Society B*, **273**, 1287–1292.

Cotton, S., Small, J., Hashim, R. & Pomiankowski, A. (2010) Eyespan reflects reproductive quality in wild stalk-eyed flies. *Evolutionary Ecology*, **24**, 83–95.

Cox, R.M. & Calsbeek, R. (2009) Sexually antagonistic selection, sexual dimorphism, and the resolution of intralocus sexual conflict. *American Naturalist*, **173**, 176–187.

Cox, R.M. & Calsbeek, R. (2010) Severe costs of reproduction persist in *Anolis* lizards despite the evolution of a single-egg clutch. *Evolution*, **64**, 1321–1330.

Craig, A.J.F.K. (1989) Tail length and sexual selection in the polygynous Long-tailed Widow (*Euplectes progne*): A cautionary tale. *South African Journal of Science*, **85**, 523–524.

Dudley, R. (2000) *The Biomechanics of Insect Flight*. Princeton University Press, Princeton, NJ.

Dudley, R. (2002) Mechanisms and implications of animal flight maneuverability. *Integrative and Comparative Biology*, **42**, 135–140.

Egge, A.R., Brandt, Y. & Swallow, J.G. (2011) Sequential analysis of aggressive interactions in the stalk-eyed fly *Teleopsis dalmanni*. *Behavioral Ecology and Sociobiology*, DOI: 10.1007/s00265-010-1054-5.

Ellington, C.P. (1984) The aerodynamics of hovering insect flight II. Morphological parameters. *Philosophical Transactions of the Royal Society B*, **305**, 17–40.

Emlen, D.J. (2008) The evolution of animal weapons. *Annual Review of Ecology, Evolution, and Systematics*, **39**, 387–413.

Endler, J.A. (1983) Natural and sexual selection on color patterns in poeciliid fishes. *Environmental Biology of Fishes*, **9**, 173–190.

Evans, M.R. (1998) Selection on swallow tail streamers. *Nature*, **394**, 233–234.

Evans, M.R. & Hatchwell, B.J. (1992) An experimental study of male adornment in the scarlet-tufted malachite sunbird: II. The role of the elongated tail in mate choice and experimental evidence for a handicap. *Behavioral Ecology and Sociobiology*, **29**, 421–427.

Evans, M.R. & Thomas, A.L.R. (1992) The aerodynamical and mechanical effects of elongated tails in the scarlet-tufted malachite sunbird: measuring the cost of a handicap. *Animal Behaviour*, **43**, 337–347.

Földvári, M., Pomiankowski, A., Cotton, S. & Carr, M. (2007) A morphological and molecular description of a new *Teleopsis* species (Diptera: Diopsidae) from Thailand. *Zootaxa*, **1620**, 37–51.

Fry, S.N., Sayaman, R. & Dickinson, M.H. (2003) The aerodynamics of free flight maneuvers in *Drosophila*. *Science*, **300**, 495–498.

Getty, T. (1998) Handicap signalling: when fecundity and viability do not add up. *Animal Behaviour*, **56**, 127–130.

Getty, T. (2006) Sexually selected signals are not similar to sports handicaps. *Trends in Ecology and Evolution*, **21**, 83–88.

Grafen, A. (1990) Biological signals as handicaps. *Journal of Theoretical Biology*, **144**, 517–546.

Hingle, A., Fowler, K. & Pomiankowski, A. (2001) Size-dependent mate preference in the stalk-eyed fly *Cyrtodiopsis dalmanni*. *Animal Behaviour*, **61**, 589–595.

Hurd, P.L. (1997) Is signalling of fighting ability costlier for weaker individuals? *Journal of Theoretical Biology*, **184**, 83–88.

Irschick, D.J., Meyers, J.J., Husak, J.F. & Le Galliard, J.F. (2008) How does selection operate on whole-organism functional performance capacities? A review and synthesis. *Evolutionary Ecology Research*, **10**, 177–196.

Jennions, M.D., Møller, A.P. & Petrie, M. (2001) Sexually selected traits and adult survival: a meta-analysis. *Quarterly Review of Biology*, **76**, 3–36.

Kingsolver, J.G., Hoekstra, H.E., Hoekstra, J.M., Berrigan, D., Vignieri, S.N., Hill, C.E., Hoang, A., Gibert, P. & Beerli, P. (2001) The strength of phenotypic selection in natural populations. *American Naturalist*, **157**, 245–261.

Kirkpatrick, M. (1987) Sexual selection by female choice in polygynous animals. *Annual Review of Ecology and Systematics*, **18**, 43–70.

Kotiaho, J.S. (2001) Costs of sexual traits: a mismatch between theoretical considerations and empirical evidence. *Biological Reviews*, **76**, 365–376.

Kruesi, K. & Alcaraz, G. (2007) Does a sexually selected trait represent a burden in locomotion? *Journal of Fish Biology*, **70**, 1161–1170.

Kullberg, C., Houston, D.C. & Metcalfe, N.B. (2002) Impaired flight ability – a cost of reproduction in female blue tits. *Behavioral Ecology*, **14**, 575–579.

Lailvaux, S.P., Hall, M.D. & Brooks, R.C. (2010) Whole-organism performance is no proxy for genetic quality: trade-offs between locomotion, attractiveness and life history in crickets. *Ecology*, **91**, 1530–1537.

Lailvaux, S.P. & Kasumovic, M.M. (2010) Defining individual quality over lifetimes and selective contexts. *Proceedings of the Royal Society B*, **278**, 321–328.

Lande, R. (1980) Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution*, **33**, 292–305.

Lande, R. & Arnold, S.J. (1983) The measurement of selection on correlated characters. *Evolution*, **37**, 1210–1226.

Langerhans, R.B., Layman, C.A. & DeWit, T.J. (2005) Male genital size reflects a trade off between attracting mates and avoiding predators in two live-bearing fish species. *Proceedings of the National Academy of Sciences, USA*, **102**, 7618–7623.

Maynard Smith, J. & Harper, D. (2003) *Animal Signals*. Oxford University Press, Oxford.

Møller, A.P. (1996) The cost of secondary sexual characters and the evolution of cost-reducing traits. *Ibis*, **138**, 112–119.

Møller, A.P., de Lope, F. & López Caballero, J.M. (1995b) Foraging costs of a tail ornament: Experimental evidence from two populations of barn swallows *Hirundo rustica* with different degrees of sexual size dimorphism. *Behavioral Ecology and Sociobiology*, **37**, 289–295.

Møller, A.P., de Lope, F. & Saino, N. (1995a) Sexual selection in the barn swallow *Hirundo rustica*. VI. Aerodynamic adaptations. *Journal of Evolutionary Biology*, **8**, 671–687.

Møller, A.P., Barbosa, A., Cuervo, J.J., de Lope, F., Merino, S. & Saino, N. (1998) Sexual selection and tail streamers in the barn swallow. *Proceedings of the Royal Society B*, **265**, 409–414.

Nicoletto, P.F. (1991) The relationship between male ornamentation and swimming performance in the guppy, *Poecilia reticulata*. *Behavioral Ecology and Sociobiology*, **28**, 365–370.

Oufiero, C.E. & Garland Jr, T. (2007) Evaluating performance costs of sexually selected traits. *Functional Ecology*, **21**, 676–689.

Panhuis, T.M. & Wilkinson, G.S. (1999) Exaggerated male eye span influences contest outcome in stalk-eyed flies (Diopsidae). *Behavioral Ecology and Sociobiology*, **46**, 221–227.

Park, K.J., Rosén, M. & Hedenström, A. (2001) Flight kinematics of the barn swallow (*Hirundo rustica*) over a wide range of speeds in a wind tunnel. *Journal of Experimental Biology*, **204**, 2741–2750.

Pocklington, R. & Dill, L.M. (1995) Predation on females or males: who pays for bright male traits? *Animal Behaviour*, **49**, 1122–1124.

Reznick, D. (1985) Costs of reproduction: an evaluation of the empirical evidence. *Oikos*, **44**, 257–267.

Ribak, G. & Swallow, J.G. (2007) Free flight maneuvers of stalk-eyed flies: do eye-stalks affect aerial turning behavior? *Journal of Comparative Physiology A*, **193**, 1065–1079.

Ribak, G., Pitts, M.L., Wilkinson, G.S. & Swallow, J.G. (2009) Wing shape, wing size, and sexual dimorphism in eye-span in stalk-eyed flies (Diopsidae). *Biological Journal of the Linnean Society*, **98**, 860–871.

Rohwer, S. (1977) Status signaling in Harris' sparrows: some experiments in deception. *Behaviour*, **61**, 107–129.

Royle, N.J., Metcalfe, N.B. & Lindstrom, J. (2006) Sexual selection, growth compensation and fast-start swimming performance in Green Swordtails, *Xiphophorus helleri*. *Functional Ecology*, **20**, 662–669.

Ryan, M.J. (1988) Phenotype, genotype, swimming endurance and sexual selection in a Swordtail (*Xiphophorus nigrensis*). *Copeia*, **1988**, 484–487.

Searcy, W.A. & Nowicki, S. (2005) *The Evolution of Animal Communication: Reliability and Deception in Signaling Systems*. Princeton University Press, Princeton, NJ.

Shine, R. (1980) "Costs" of reproduction in reptiles. *Oecologia*, **46**, 92–100.

Small, J., Cotton, S., Fowler, K. & Pomiankowski, A. (2009) Male eyespan and resource ownership affect contest outcome in the stalk-eyed fly, *Teleopsis dalmanni*. *Animal Behaviour*, **78**, 1213–1220.

Swallow, J.G., Wilkinson, G.S. & Marden, J.H. (2000) Aerial performance of stalk-eyed flies that differ in eyespan. *Journal of Comparative Physiology B*, **170**, 481–487.

Tomkins, J.L., Kotiaho, J.S. & LeBas, N.R. (2005) Phenotypic plasticity in the developmental integration of morphological trade-offs and secondary sexual trait compensation. *Proceedings of the Royal Society B*, **272**, 543–551.

Weis-Fogh, T. (1973) Quick estimates of flight fitness in hovering animals, including novel mechanisms for lift production. *Journal of Experimental Biology*, **59**, 169–230.

Wilkinson, G.S. (1993) Artificial sexual selection alters allometry in the stalk-eyed fly *Cyrtodiopsis dalmanni* (Diptera: Diopsidae). *Genetical Research*, **62**, 213–222.

Wilkinson, G.S. & Dodson, G.N. (1997) Function and evolution of antlers and eye stalks in flies. *The Evolution of Mating Systems in Insects and Arachnids* (eds J. Choe & B. Crespi), pp. 310–328. Cambridge University Press, Cambridge.

Wilkinson, G.S., Kahler, H. & Baker, R.H. (1998) Evolution of female mate preferences in stalk-eyed flies. *Behavioral Ecology*, **9**, 525–533.

Wilkinson, G.S. & Taper, M. (1999) Evolution of genetic variation for condition dependent ornaments in stalk-eyed flies. *Proceedings of the Royal Society B*, **266**, 1685–1690.

Worthington, A.M. & Swallow, J.G. (2010) Gender differences in survival and antipredatory behavior in stalk-eyed flies. *Behavioral Ecology*, **21**, 759–766.

Zahavi, A. (1975) Mate selection – a selection for a handicap. *Journal of Theoretical Biology*, **53**, 205–214.

Supporting Information

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

Table S1. Eyespan, wing length and wing area were all significantly related to body length in seven species of stalk-eyed flies. Results are shown from regressions of each trait (log-transformed) on log-transformed body length.

Table S2. Results from ANCOVAs, showing tests for sexual dimorphism in wing length for seven species of stalk-eyed flies. We did not test the main effect of sex for those with significantly heterogeneous slopes (i.e. a significant body length*sex interaction).

Table S3. Correlations between relative eyespan and relative wing length in seven species of stalk-eyed flies. Significant correlations ($P < 0.05$) are in bold.

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