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Gender differences in survival and antipredatory behavior in stalk-eyed flies

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Exaggerated eye span of stalk-eyed flies is a classic example of the evolution of an extravagant male ornament resulting from sexual selection. Increased male eye span may entail costs associated with production and/or maintenance, including potential locomotor costs that may increase predation risk. However, behavioral responses by individuals may alter the relationship between a morphological trait and performance, increasing expected overall fitness. Antipredator behavior and survival of male and female *Teleopsis dalmanni* were quantified during pairwise interactions between individual flies and an actively foraging, generalist arachnid predator (*Phidippus audax*). Male and female flies were compared under the assumption that female stalk length is closer to the optimum set by natural selection. There were significant differences in behaviors between the sexes, with males spending more time engaged in aggressive actions. Interestingly, males also exhibited increased survival relative to females. Within males, survivors did not differ from nonsurvivors in any of the morphological measures, including eye span, but there was a significant difference in abdomen bobbing, grooming, and flight. These results highlight the importance of behavior in the ability of stalk-eyed flies to effectively elude predators, but they do not support the hypothesis that male stalk-eyed flies suffer increased predation due to exaggerated eyestalks. *Key words:* antipredator behavior, predation risk, sexual selection, stalk-eyed flies. *[Behav Ecol 21:759–766 (2010)]*

Sexual selection is a process that favors traits beneficial in female mate choice or male–male competition (Andersson 1994), many times resulting in the evolution of exaggerated morphologies in males. It is well accepted, however, that sexually selected traits are often opposed by natural selection and, thus, do not evolve without limits (Fisher 1930; Kotiaho 2001). Possible costs of such traits include reduced foraging ability (Møller and de Lope 1994; Bokony et al. 2008), locomotor disadvantages (Evans and Thomas 1992; Barbosa and Møller 1999), and/or production or maintenance costs (Basalo and Alcaraz 2003; Allen and Levinton 2007). Because such measures are merely components of whole-organism fitness, however, they may not translate directly into survival, unlike measurement of predation risk. Predation risk is a robust, whole-organism measurement of fitness because it has obvious fitness consequences associated with it (Kotiaho et al. 1998; Stuart-Fox et al. 2003) making it evolutionarily significant (Vanhooydonck et al. 2007). A negative correlation between ornament size and survival has been found in numerous species that experience strong directional sexual selection (Moodie 1972; Kotiaho et al. 1998; Stuart-Fox et al. 2003; Basalo and Wagner 2004). This intuitive trend is consistent with the notion that sexual selection may create traits that cause reduced locomotor performance. Such traits would then be opposed by natural selection acting to minimize traits with costs and enhance overall locomotor performance (Provost et al. 2006).

Based on the results of a recent meta-analysis, however, negative correlations between male ornaments and survival may be less widespread than previously thought. Jennions et al. (2001) uncovered a greater number of studies indicating that individuals with larger ornaments actually have prolonged survival. This counterintuitive result could be explained by the condition-dependent expression of secondary sexual traits, which honestly signal genetic or phenotypic quality. If males with superior underlying environmental or genetic viability are better able to bear the production and/or maintenance costs associated with the exaggerated trait, they may then actually experience higher probabilities of survival (Zahavi 1975, 1977; Andersson 1986; Iwasa et al. 1991). In such cases, because traits are more costly for low-quality than high-quality individuals to bear, a positive relationship between trait exaggeration and longevity is observed (Price et al. 1993; Møller and de Lope 1994; Grether 1997; Hoglund and Sheldon 1998). Another possible explanation for this positive relationship is that organisms exhibiting secondary sexual traits may experience natural selection in an early life stage but in later life stages do not experience differential survival due to the secondary sexual trait. For example, during the development of secondary sexual traits, production costs may be high and therefore may entail tradeoffs between larval growth and ornament size (Knell et al. 1999; Nowicki et al. 2002). Once developed, however, the costs associated with maintaining these structures may be minimal so that a difference in survival among individuals with differing ornaments is no longer observable.

Natural selection on morphological traits is widely believed to act most directly on whole-organism performance (Arnold 1983; Irschick and Garland 2001; Irschick et al. 2008), but there may be alternative mechanisms that significantly affect survival, such as altered behavioral responses or physiological condition (Irschick 2002). Behavior is an important link between an organism's physiological performance and Darwinian fitness and, therefore, must be considered when studying the survival costs of a sexually selected trait (Gibbs 1999; Oufiero and Garland 2007). Previous studies have shown that morphology alone is not always the most accurate predictor of performance and fitness (Lauder 1996; Wainwright et al. 2005), many times because behavior has been adjusted to control for negative effects and compensate for performance deficiencies

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(Garland and Carter 1994; Hedrick 2000; Jennions et al. 2001; Husak and Fox 2006). Thus, by altering behavior, animals can change the relationship between a morphological trait and performance, in turn affecting overall fitness (Irschick 2002; Irschick et al. 2007). For example, antipredator behaviors, such as defensive mechanisms or escape strategies, may influence a predator's prey selection by increasing foraging cost, decreasing net energy intake, or decreasing attack success rate (Provost et al. 2006). This suggests that even in the event that a trait does impose constraints (e.g., locomotor), survival of organisms may, in many cases, actually rely more heavily on that organism's behavior.

Stalk-eyed flies of the family Diospidae are ideal model organisms for studies of sexual selection and costly exaggerated ornaments. All species in this family exhibit hypercephaly, a type of exaggerated head morphology in which the eyes and antennae are displaced laterally on long peduncles. Eye span is heritable (Wilkinson and Taper 1999), and hence subject to both sexual and natural selection (Wilkinson 1993). Both female preference (Wilkinson and Reillo 1994) and male–male competition for copulation sites (Panhuis and Wilkinson 1999) have played a role in the evolution and maintenance of this extravagant ornament. Though it is often assumed that these elaborate eyestalks are associated with production and/or maintenance costs, few explicit tests of such tradeoffs exist (Wilkinson 1993; Swallow et al. 2000), and no research has been performed to measure antipredator behavior of these flies or predation risk associated with the eyestalks. Studies on flight mechanics suggest that males, especially with larger eye span, may have impaired flight abilities when compared with females (Swallow et al. 2000). Although morphological compensation may minimize some of the costs associated with eyestalks in flight (Ribak and Swallow 2007; Ribak et al. 2009), even slight locomotor impairment may have an effect on Darwinian fitness through predation (reviewed in Oufiero and Garland 2007).

We staged interactions between stalk-eyed flies and a generalist predator to determine whether differences in eye span and antipredator behavior affected predation risk. We used 2 approaches to examine the roles of eye span and behavior in predicting survival, the first being intersexual comparisons of males and females in the sexually dimorphic species *Teleopsis dalmanni.* Because eye span is more exaggerated in males of sexually dimorphic species and is thought to be a costly trait, differences in survival and behavior can be compared with females of the same species under the general assumption that the female trait is nearer to the optimum set by natural selection (Haas 1976; Lande 1980; Anholt 1997). Under a Fisherian model of selection, males would incur a greater predation risk than females due to their larger ornaments; however, enhanced male survival could suggest several other alternatives. The presence of eyestalks may be cost neutral for adult flies; alternatively, flies may compensate for any costs present through other mechanisms.

Next, we used intrasexual comparisons of males to examine whether variation in eye span and/or behavior among males plays a significant role in survival. Increased predation risk in males with larger eyestalk length would support sexually selected ornaments being associated with fitness costs; alternatively, behavioral differences that correlate with morphological measurements and result in equal or even decreased predation risk would suggest direct behavioral compensation for the exaggerated male ornament. Another possibility is that eye span will not predict survival and morphology will not correlate with behavioral traits. This would suggest that antipredator behavior is most important for survival and that there is little to no predation cost of exaggerated eyestalks.

MATERIALS AND METHODS

Study organisms

Teleopsis dalmanni used in this experiment were descendants of pupae obtained from a large stock population currently maintained at the University of Maryland at College Park. Male and female flies were housed together in 40 × 20 × 22 cm clear plastic containers lined with moist cotton and blotting paper and kept at 26 °C on a 12:12 h light:dark cycle. The flies were reared in age cohorts based on eclosion date and were provided pureed corn supplemented by *Drosophila* medium. Sexual maturity in *T. dalmanni* is reached after 1 week but peaks at 4 weeks after eclosion (Reguera et al. 2004). To ensure that fully mature flies of similar age and experience were being compared, we only used flies from the 4–8 week cohorts.

We used the bold jumping spider (*Phidippus audax*) as our predator. These spiders from the family Salticidae are generalist, actively foraging predators that have unique complex eyes (Land 1969) which they use to guide them in prey choice decisions (Jackson et al. 2005). The use of a vision-based predator is important when assessing the effects of a conspicuous morphological trait, as well as prominent antipredatory behavior, on predation risk. Additionally, salticids have worldwide distribution, meaning that, although the specific species used in this study may not be a natural predator of stalk-eyed flies, another closely related species likely is (Zhang and Song 2003). In preliminary trials, *P. audax* paired with stalk-eyed flies readily pursued, captured, and ingested them; stalk-eyed flies readily acknowledged and oriented antipredatory behaviors toward the spiders as well, demonstrating the predator's ability to create the response necessary for this study.

We collected mature and juvenile *P. audax* from the sides of buildings and within fields consisting mainly of tallgrasses near The University of South Dakota, Vermillion, SD. We separately maintained mature spiders until they created an egg sac and then released them back to their original collection site. We reared the resulting hatchlings (ca. 50–60 spiderlings per egg sac) collectively in a 40 × 20 × 22 cm clear plastic container with multiple corn husks for structure and an abundant supply of moist cotton, fruit flies, and pinhead crickets. After 8 weeks, we separated and housed each spider individually in a small plastic petri dish, identical to those of the collected adults. After separation, we provided all juvenile spiders with moist cotton and a constant supply of 3–6 mm crickets. We note that the collective housing of hatchlings deviated from standard rearing methods, which advise housing spiders separately to prevent cannibalism (Brown 1946; Jackson 1974). Grouping young simplified rearing and greatly increased the survival rate from less than 50% when reared individually to more than 90% (Worthington A, personal observation). Although outside the scope of this study, it is worth investigating this new rearing method of salticids in the future due to their extensive use in research.

Creating the ethogram

We developed an ethogram of stalk-eyed fly behaviors by observing 20 h of flies performing activities in the presence of a predator and included the following behaviors: grooming (eyestalks, wings, forelegs, and hind legs), directly walking toward predator, flying toward predator, fast-walking retreat from predator, flying away from predator, displaying forelegs, and abdomen bobbing. The ethogram also included behaviors and outcomes of direct interaction with the predator: jabbing predator with forelegs, fly pounced on by spider, fly caught by spider, fly escaping from predator's grasp, and fly death. For a more detailed description of each behavior, see Table 1.

Table 1

Ethogram of behaviors scored during predation interactions

Behavior	Description
Offensive	
Walking approach	Fly approaches spider with eyestalks parallel
Flying approach	Flight initiated and directed toward spider
Abdomen bobbing	Abdomen lifted up and down at high frequency
Jabbing predator	Forelegs used to jab body of predator
Displaying forelegs	Raised on hind legs with forelegs spread wide in air making large sweeping circles
Grooming eyestalks	Tarsi of front legs used to stroke the eyestalks from head to tip; either both tarsi stroke same eyestalk or with each tarsus stoking different eyestalks
Defensive	
Walking retreat	Fly walks quickly from spider's immediate presence
Flying retreat	Flight initiated away from spider
Escape	Fly frees itself after being caught by spider
Displacement	
Flying random	Nonpredator related flight
Grooming wings	Wings spread upward and stroked by hind tarsi
Grooming forelegs	Front leg tarsi rubbed together
Grooming hindlegs	Hind leg tarsi rubbed together with abdomen lifted
Spider actions	
Spider retreat	Spider retreats from approaching fly
Spider attack	Spider attempts to pounce on fly
Spider catch	Spider maintains fly in its grasp after pouncing
Eaten/fly death	Fly does not escape spider's grasp and is eaten

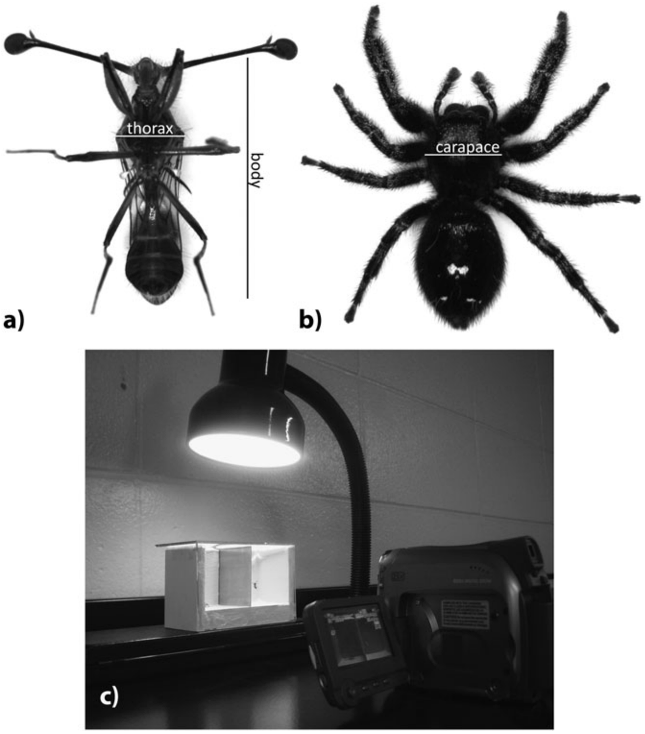

Figure 1
a) Male *Teleopsis dalmanni* lying on dorsal side for marked measurements of eye span, body length, and thorax width. (b) Arachnid predator *Phidippus audax* with marked measurement of carapace width. (c) Experimental set up of arena, lighting, and video camera.

Experimental techniques

To determine whether behavior between and within sexes differ in *T. dalmanni*, we individually matched 61 males and 22 females of varying sizes against a naive arachnid predator in a small microcosm. The arena was a 10 × 5 × 5–cm wooden box lined with cotton and moist blotting paper with 2 sides of glass separated by a metal partition (Figure 1c). This was large enough to allow for ready flight but small enough to force mutual awareness and interaction between the fly and spider. We staged all interactions from 1000 to 1400 h. In preparation for an interaction, we standardized predator hunger by allowing each spider to feed until sated on small brown crickets and then depriving them of food for a period of 7 days (Nelson and Jackson 2006). This extended starvation period ensured that each spider would pursue the fly with which it was paired (Nelson et al. 2005).

Prior to introducing the fly to the naive spider, we anesthetized each fly and spider with CO_2 and photographed them under a dissection microscope at ×15–20 magnification to take standard body measurements to the nearest 0.01 mm using Scion Image. For the flies, these measurements included eyestalk length (from outer edge of the ommatidia), thorax width (widest point of the thorax), and total body length (from front of face to wing tip) (Figure 1a; Wilkinson 1993). According to final measurements, sexes differed in eye span and residual eye span but not thorax width or body length (Table 2).

Spider measurements included carapace length and width and abdomen length and width (widest and longest points; Figure 1b). All measures of spider size were correlated with carapace width (carapace length: $r = 0.87$, $P < 0.0001$; abdomen width: $r = 0.56$, $P < 0.0001$; abdomen length: $r = 0.60$, $P < 0.0001$; $n = 83$). Therefore, we used carapace width to standardize spider size because it was the most reliable index of age. Additionally, unlike abdomen dimensions that change in relation to starvation and desiccation, carapace width is hardened exoskeleton and not affected by daily condition. Only spiders with carapace widths between 2.50 mm and 3.50 mm (mean ± standard error: 2.94 ± 0.27, range: 2.49–3.41 mm) were used in interactions. Spiders smaller than 2.50 mm appeared reluctant to engage in interactions with stalk-eyed flies even though they are known to capture and consume prey several times larger than themselves. Similarly, spiders much larger than 3.50 mm rarely pursued the flies, possibly because larger spiders were less affected by the 7-day starvation period.

After recording measurements, we placed the spider and fly in an arena on opposite, randomly selected sides and allowed them to remain there undisturbed in a climate-controlled room of 26 °C. After 24 h of acclimatization, a 25-watt bulb lighted the arena from above and a Canon ZR500 handheld digital camcorder filmed the interaction with the entire arena in its field of view. We removed the partition and left the room to eliminate any observer bias. Filming was allowed to proceed until either the spider caught the fly without it escaping or until 20 min had passed. We utilized the prepared ethogram to score the behaviors during each interaction using the free event recorder JWatcher (Blumstein et al. 2006). We then determined the frequency and proportion of time engaged in each behavior. Only trials that exhibited intense interactions between fly and spider, where the fly was actively

Table 2

Mean ± standard deviation of morphological measurements and behavioral differences of male and female *Teleopsis dalmanni*

Measurement	♂	♀	Significance test
Fly size (mm)			
Eye span	7.94 ± 0.53	5.71 ± 0.16	$F_{1,81} = 368.84$***
Body length	6.75 ± 0.31	6.69 ± 0.22	$F_{1,81} = 0.80$
Thorax width	1.84 ± 0.10	1.83 ± 0.08	$F_{1,81} = 0.29$
Residual eye span	1.17 ± 0.04	0.85 ± 0.02	$F_{1,81} = 1489.31$***
Frequency of behaviors (no./min)			
Jabbing predator	0.06 ± 0.15	0.00 ± 0.02	$F_{2,80} = 7.94$[a]
Flying retreat	0.38 ± 0.68	0.15 ± 0.25	$F_{3,79} = 6.72$[a]
Walking retreat	0.57 ± 0.62	0.67 ± 0.83	$F_{4,78} = 6.09$[a]
Proportion of time involved in behavior			
Abdomen bobbing	1.14 ± 0.41	0.81 ± 0.48	$F_{1,81} = 9.09$*,[a]
Duration	16.30 ± 6.72	11.06 ± 8.86	$t_{81} = -2.87$*
Survival	75.41%	50.00%	$\chi_1^2 = 6.61$**

All reported values have a sample size of 61 for males and 22 for females.

Asterisks denote statistical significance in the difference between sexes for the given variable (*$P < 0.05$; **$P < 0.001$; ***$P < 0.0001$).

[a] Denotes behaviors included in final stepwise discriminant analysis model; see Figure 2

pursued by the jumping spider, were used in this analysis. This was done in order to remove the effect of spider/fly activity levels as some trials proved to have presumably unhealthy flies (possibly due to desiccation or disease) or spiders that were uninterested in pursuing the available prey.

Statistical analysis

First, to test the relationship between sex and all behavioral variables, we conducted a multivariate analysis of variance (MANOVA) using SAS 9.1.3 PROC GLM. We then conducted a stepwise discriminant analysis using SAS 9.1.3 PROC STEPDISC to examine where the largest amount of variance between the sexes existed, allowing us to determine which behaviors most accounted for the behavioral differences. All proportions were arcsine-square root transformed before being subjected to statistical analysis. Lastly, we examined sex differences in predation risk and survival directly. First, we compared contest duration of male *T. dalmanni* with that of females using a 2-sample *t*-test. Then, we used a chi-square analysis to determine if sexes differed in overall survival rates, which is a direct measure of predation risk.

To examine the influence of ornament size on survival in males, morphological differences (eye span, body size, thorax width, and residual eye span) of males that survived versus those that perished were analyzed using MANOVA. Because eye span and body length are highly correlated ($r = 0.91$, $P < 0.0001$, $n = 61$), eye span residuals were included (calculated as the ratio of eye span to body length), with larger residuals representing males with eye spans greater than would be expected for their body size. We used Pearson's correlation to determine whether the frequency of any behaviors correlated specifically with eye span, residual eye span, or body size. Significance levels were corrected with the sequential Bonferroni technique using an experiment-wise error rate of $\alpha = 0.05$. Lastly, stepwise multiple logistic regression was used to examine how variation in antipredator behavior predicted survival among males. All statistic analyses were done in SAS 9.1.3 (SAS Institute Inc. 2002–2004).

RESULTS

Intersexual behavioral and survival differences

The MANOVA revealed a significant sex effect (Wilks' $F_{14,68} = 2.84$, $P = 0.0021$), indicating that males and females differed in their behavioral responses to predators. According to the discriminant analysis, this difference appeared to be driven primarily by males spending a larger proportion of time abdomen bobbing than females ($F_{1,81} = 9.09$, $P = 0.0034$), frequency of jabbing predator ($F_{2,81} = 7.94$, $P = 0.0148$), frequency of predator avoidance by flying ($F_{3,79} = 6.72$, $P = 0.0572$), and frequency of predator avoidance by walking ($F_{4,78} = 6.09$, $P = 0.0630$), all of which were higher in males relative to females, except walking retreat from predator, which showed the opposite pattern (Table 2 and Figure 2).

Analysis of survival showed that sexes differed in both the duration of the interaction and probability of evading predation when in close proximity to a predator (Figure 3). Males, on average, survived approximately 50% longer than females ($t_{81} = -2.87$; $P = 0.0052$). Analysis of susceptibility of predation risk was measured by comparing the number of males and females that ultimately survived the predation encounter. In 46 of 61 trials analyzed, males survived the entire 20 min, as compared with only 10 of 22 females (Figure 3). A chi-square test indicated that males had significantly higher survival than did females ($\chi_1^2 = 6.61$, $P = 0.0101$). Two-sample *t*-tests confirmed that males and females did not differ in the number of times pounced on by the spider ($P = 0.4415$), the number of times caught by the spider ($P = 0.3075$), or the probability of escaping after being caught ($P = 0.4868$); so we were unable to attribute differences in survival to spider behavior, activity, or differential behavior after capture.

Intrasexual behavioral and survival differences

MANOVA results revealed that surviving males did not differ from nonsurviving males in eye span ($F_{1,61} = 0.00$; $P = 0.9458$), body length ($F_{1,61} = 0.03$; $P = 0.8658$), thorax width ($F_{1,61} = 1.23$; $P = 0.2713$), or residual eye spans ($F_{1,61} = 0.08$; $P = 0.7729$). Neither survival duration nor the frequency of any individual behaviors significantly correlated with any of the measures of body size, even without conservative Bonferroni correction. However, logistic regression did reveal an overall significant effect of antipredator behavior in predicting male survival ($\chi_1^2 = 59.8629$, $P = 0.0001$). Logistic regression detected significant effects for several behaviors, with surviving males spending a larger proportion of time abdomen bobbing ($P = 0.0197$). Nonsurviving males initiated flight more frequently than did surviving males ($P = 0.0090$).

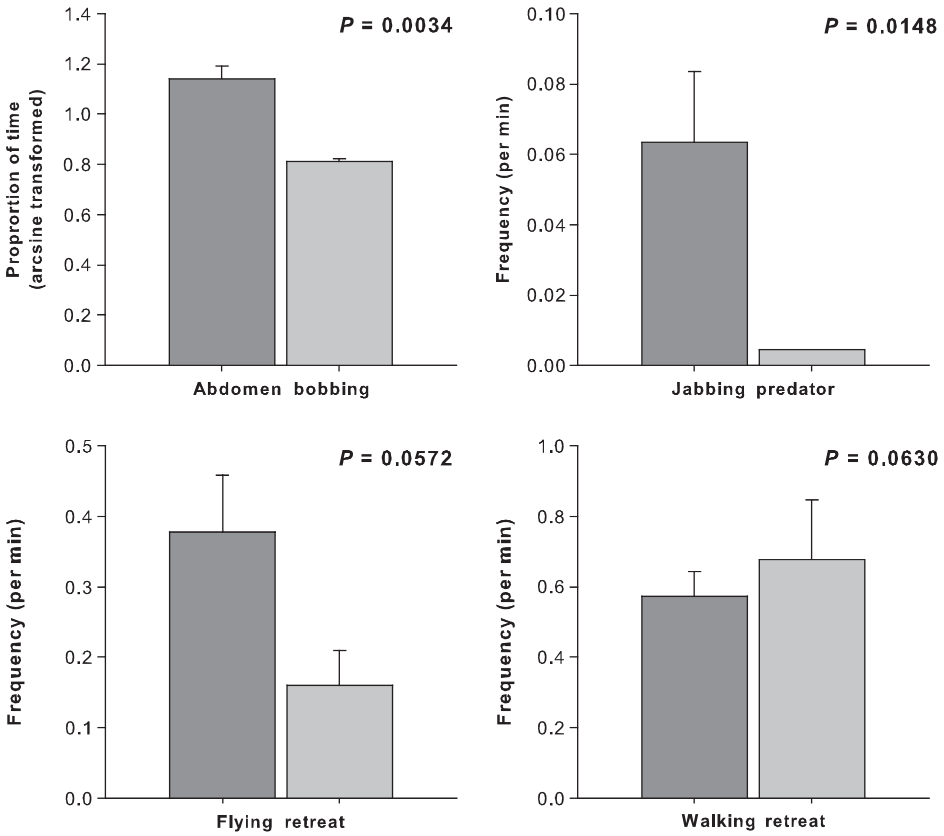

Figure 2
Mean ± standard error of significant variables from a stepwise discriminant analysis of behaviors of males (dark gray) and females (light gray) with corresponding *P* values.

DISCUSSION

We found a strong difference in survival between the sexes, with females suffering much higher mortality than males. Female eye span is thought to be closer to the optimum set by natural selection and their smaller eye span, therefore, should not impose a greater cost than the larger eye span of males. Additionally, no differences in eye span, body size, or thorax width separated surviving and nonsurviving males, suggesting that males with larger eye spans do not incur a greater predation risk, supporting the alternative hypothesis that eyestalks may not impose large costs in adult flies.

In order to adequately film and document the behaviors of interest in this study, a small microcosm was necessary to provide the resolution needed to observe fly behavior. Forcing the predator and fly into close proximity to document behavior possibly inflated predation risk beyond natural conditions. Escaping from the immediate proximity of a predator is the easiest way to avoid becoming prey; however, due to the small arena size, this evasive action may not have been as successful as it would have been in nature. Conversely, we do not believe that this would be the cause for the disparity between male and female survival. Although nonsignificant, males actually employed flight as an escape mechanism more so than did females; if decreased escape effectiveness by flight was the reason behind increased predation, males would have exhibited lower survival rates than females. With antipredatory behaviors now documented and examined, larger mesocosm studies can be pursued to allow flies more effective use of flight and other predator avoidance mechanisms to examine this effect further

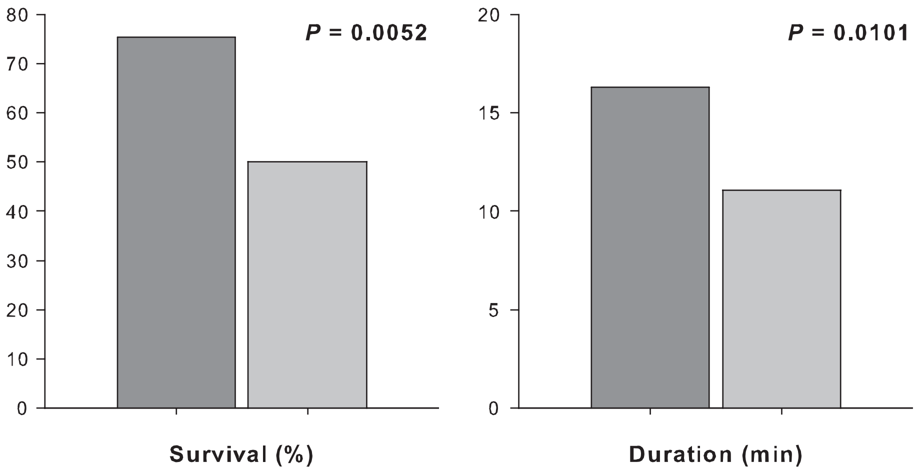

Figure 3
Survival and duration differences between males (dark gray) and females (light gray).

and gain a better understanding of what affects predator evasion in stalk-eyed flies.

Previous studies support condition dependence of ornament expression in stalk-eyed flies. When males and females are raised with varying amounts of resources, males show a much stronger effect of condition dependence, in terms of both absolute and relative eyestalk length. In males, larval condition explained 40–68% of the variance in trait size (David et al. 1998). Studies of male–male competition also support condition dependence, with residual eye span being a significant predictor of fight outcome. Here, males use eye span as an honest signal of body size in order to determine the likelihood of winning a fight over resources (Panhuis and Wilkinson 1999). Observations of adult longevity have also been shown to correlate with increasing eye span within laboratory-reared populations (Wilkinson et al. 2006) and with increasing body size in field-caught flies (Wilkinson and Reillo 1994). The results from the current study agree with but do not provide additional support per se for condition dependence. Although males with greater eye span did not exhibit increased survival relative to smaller eye span males, equal survival among all males suggest that males with larger ornaments either do not incur higher costs or are better able to bear the costs due to their better quality.

Costs of sexually selected traits are considered crucial for establishing limits on the expression of exaggerated traits (Andersson 1994). If predation risk does not set this limit, what other direct fitness costs need to be considered? Studies on *Drosophila melanogaster* suggest survival costs earlier in life may be important. These studies found that larger bodied males have higher fecundity but that larval mortality increases with body size (Wilkinson 1987; Partridge and Fowler 1993). Therefore, although natural selection favors large-bodied flies in adulthood, body size is selected against during development. Similar evidence has been recorded for larval mortality and large eye span in stalk-eyed flies. In stalk-eyed flies artificially selected for eye span, lines with increased eye span took on average one day longer to develop than unselected lines and also had fewer large pupae eclose than intermediate sized pupae (Wilkinson 1993). If this is indicative of natural selection, then larger viability tradeoffs may occur earlier in life and, therefore, males that survive to adulthood have higher fitness both in terms of increased mating success and increased longevity.

Our experiment also revealed that antipredator behaviors vary between the sexes in stalk-eyed flies. Abdomen bobbing is generally the first behavior exhibited when a perceived threat is near (Worthington A, personal observation), and males spent a larger proportion of time exhibiting this behavior than did females. Although its function is unknown, it may play a role in predator deterrence or serve as a threat display to predators, hence decreasing predation risk. Males also approached and physically jabbed the spider more frequently. Such behavior can be viewed as possible predator inspection, which has been shown in several studies to actually decrease predator pursuit of prey (Dugatkin and Godin 1992; Pitcher 1992; Vega-Redondo and Hasson 1993). In guppies, predator approach and inspection decrease the probability of being attacked, possibly because the prey conspicuously advertise their awareness of the predator, informing the predator that the element of surprise has been lost and pursuit is likely to be unprofitable (Godin and Davis 1995). These differences in behavior may cause further predation risk divergence between the sexes. Overall, male survival may be due more to behavioral differences than eye span. The results of the intrasexual comparisons, in accordance with results from the intersexual comparisons, show that surviving males spent a larger proportion of time abdomen bobbing compared with nonsurviving males, stressing its importance in antipredator display. Because no correlations between body measurements and behaviors were found, it is unlikely that behavior is being use to compensate specifically for the costs of larger eye spans.

As demonstrated by this study, specific behaviors are critical components of antipredator responses that must be included, in addition to morphological measures, in studies of fitness tradeoffs of sexually selected traits. Natural selection acting on increasing maximum performance ability might do so through behavior rather than on the traits that actually affect individual performance. Thus, indirect evolution of a behavioral trait can substitute for the direct evolution of a trait affecting performance (Gibbs 1999). Behavioral mechanisms are documented in many taxa with sexual signals to deal with the costs of predation (Zuk and Kulluru 1998). For example, male crickets that use auditory signals during courtship become more cautious toward predators, remaining hidden for a longer period of time after a disturbance by a perceived threat (Hedrick 2000). Such mechanisms seem to play a role in stalk-eyed flies, where males investigate a predator and acknowledge predator presence more frequently than females. Selection will favor individuals that act in a manner that maximizes fitness, so although eye span costs may be more prevalent during larval development, behavior may be a trait selected on in adults to increase viability and mitigate morphological tradeoffs.

CONCLUSIONS

Stalk-eyed flies have evolved exaggerated ornaments through sexual selection, yet males with large eye spans do not appear to have a higher predation risk, and males in general fare better when faced with a predator than do females. Additionally, behavioral differences between the sexes suggest different behavioral mechanisms are used by males and females when facing a predator and that these differences correlate with survival. Behavior is likely to explain the observed survival differences, highlighting its importance in being included in studies of performance and fitness. Studies failing to incorporate variation in behavior may be overlooking an important factor in survival (e.g., Husak 2006) and come to inaccurate conclusions about the costs of sexually selected traits. Behavior is often overlooked as it is a time consuming and difficult trait to measure; yet its significance is evident and has important effects on whole-organism performance.

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