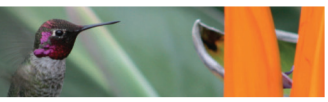
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Sequential Analysis Reveals Behavioral Differences Underlying Female-Biased Predation Risk in Stalk-Eyed Flies

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Abstract

Stalk-eyed flies are classic models of how sexual selection can drive morphological and behavioral elaboration. Exaggerated ornaments born by stalk-eyed flies could impose locomotor costs and increase susceptibility to predation; however, a previous study determined that behavior, not eye span, was the major influence on predation risk. Despite the importance of behavior, relatively little is known about how these flies avoid and deter predators. We created an ethogram of behaviors and used it to score individual interactions of male and female *Teleopsis dalmanni* paired with an actively foraging, generalist arachnid predator (*Phidippus audax*). Sequential analysis was employed to identify temporal patterns in behavior and determine how males and females differ in their approaches to avoiding predation. Our results indicate that males and females significantly differ when specific behaviors were employed. Patterns in the behavioral transitions suggest that males are more aggressive than females and are more likely to approach a predator to jab, abdomen bob, or display. Males elicited more retreat responses from the predator, whereas females elicited more attacks. Although the behavioral repertoires of male and female stalk-eyed flies are indistinguishable, their uses of the behaviors differ, particularly the sequential order of presentation, suggesting a strong sex difference in anti-predatory behavior.

Introduction

Sexual selection is responsible for the evolution of extreme morphologies used to gain access to mates (Andersson 1994). These ornaments are often conspicuous and result in increased predation risk (Stuart-Fox et al. 2003; Husak et al. 2006), ultimately leading to natural selection working in opposition to the forces that increase mate acquisition (Endler 1992; Zuk & Kolluru 1998). As a consequence of antagonistic selection, compensatory mechanisms to reduce predation risk and mortality have evolved (Husak & Swallow 2011). Morphological measurements of sexually selected traits (e.g. size or shape) are not always the most accurate predictor of fitness (Lauder 1996; Wainwright et al. 2005) many times because behavior has been altered as well (Garland & Carter 1994; Hedrick 2000; Jennions et al. 2001). Adaptive changes in behaviors exhibited near or directed at predators have a large impact on predation risk (Hedrick 2000; Fowler-Finn & Hebets 2010). Thus, behavior is an important link between an organism's physiologic performance and fitness and must be considered when studying survival costs of sexually selected traits (Gibbs 1999; Oufiero & Garland 2007).

Stalk-eyed flies are model organisms for studies on sexual selection. They are members of the Diopsidae

family and are characterized by eyes displaced laterally on long peduncles, an ornament subject to both natural and sexual selection (Wilkinson 1993). Exaggerated eye span evolved via both female choice (Wilkinson & Reillo 1994; Wilkinson et al. 1998) and male–male competition (Burkhardt & de la Motte 1983; Panhuis & Wilkinson 1999). Because eye span appears to be an honest signal of male 'quality' (Cotton et al. 2004, 2009), it may be associated with performance or developmental tradeoffs that limit eyestalk elongation. Multiple studies have examined costs of this ornament associated with flight mechanics (Swallow et al. 2000; Ribak & Swallow 2007), and the potential for morphological compensation to reduce these costs (Ribak et al. 2009; Husak & Swallow 2011; Husak et al. 2011) but only recently has a direct measure of predation risk, a major factor affecting fitness, been examined (Worthington & Swallow 2010).

Worthington & Swallow (2010) determined that stalk-eyed fly behavior, not eye span, was the determining factor of female-biased predation risk and mortality. Males survived 47% longer in the presence of a predator and experienced 50% less mortality relative to females of the sexually dimorphic stalk-eyed fly species *Teleopsis dalmanni*. Although the behavioral ethograms of the sexes were indistinguishable, differences in the proportion of time spent using specific behaviors differed. Males spent a larger proportion of time displaying anti-predator behaviors and showed greater frequency of predator inspection than did females. When comparing intra-sexual differences, surviving and non-surviving males did not differ in eye span but did show significant differences in anti-predator behaviors. Although these results indicate that male and female anti-predator behavior differs, how these differences affect predation risk requires further investigation.

Because behavior unfolds throughout time as a sequence of events or states (Slater 1973; Sackett 1979; Bakeman & Gottman 1997), taking time into account can reveal differences between groups that might not otherwise be detected by an analysis that ignores sequence (Gottman & Notarius 1978; Gottman & Roy 1990). Studies that investigate temporal patterns of behavior employ sequential analysis to address various questions, including how to classify behaviors (Slooten 1994), describe courtship mechanisms (Clark 1994; Hoikkala & Crossley 2000; Hurt et al. 2004), or investigate aggression (Chen et al. 2002; Egge et al. 2011). Sequential analysis can be used when exploring novel behavioral observations of species or contexts and provide a basic method for investigating the structure of behavior and hypothesizing the function of each action.

In this study, our goal was to characterize the temporal patterns of anti-predator behavior for both sexes of stalk-eyed flies (*T. dalmanni*) to better understand how differences in the use of behaviors may translate into increased predation risk and mortality of females. By employing sequential analysis, we can determine which behaviors elicit or inhibit predation events by an arachnid predator and elucidate whether these differences play a role in the female-biased predation risk. We expect to find that anti-predator behaviors employed by females prior to predation are different from those employed by males and that females are less effective at deterring an attack. Additionally, we explore the functions of the behaviors exhibited and suggest how employing these behaviors may help stalk-eyed flies deter predation.

Methods

Study Organisms

We studied *T. dalmanni*, a species native to the tropics of Asia. The captive-bred populations used in this experiment were descendants of pupae obtained from Gerald Wilkinson (University of Maryland at College Park). Male and female flies were housed together in clear plastic containers (40 × 20 × 22 cm) lined using moist cotton and kept at 80% humidity and 26°C on a 12-h light/dark cycle. The flies were reared in age cohorts based on eclosion date and were maintained on a diet of pureed corn supplemented with Ward's *Drosophila* medium. Flies were provided food and water *ad libitum*, and cages were furnished with hanging strings to simulate the rootlets they occupy in nature. Sexual maturity in *T. dalmanni* is reached 1 week post-eclosion but peaks at 4 weeks (Reguera et al. 2004). To ensure that only fully mature flies of similar age and experience were included, we used flies from the 4–8 week cohorts.

We used the arachnid *Phidippus audax* as our predator. Spiders from the Salticid family are generalist actively foraging predators that have a worldwide distribution (Zhang & Song 2003), so it is likely that a closely related species is a natural predator of members of Diopsidae. When paired in preliminary trials, *P. audax* readily pursued, captured, and ingested stalk-eyed flies. Additionally, *T. dalmanni* readily acknowledged and oriented anti-predatory behaviors toward *P. audax*. We collected mature *P. audax* from the sides of buildings and within fields

consisting mainly of tall grasses near The University of South Dakota, Vermillion, SD, USA. We maintained mature spiders until they produced an egg sac and then released them back to their original collection site. We reared the resulting hatchlings collectively in a clear plastic container (40 × 20 × 22 cm), providing numerous dried cornhusks for structure and an abundance of moist cotton, fruit flies, and pinhead crickets for foraging. After 8 weeks, we separated and housed spiders individually in large plastic Petri dishes where water and 3–6 mm crickets provided *ad libitum*.

Creating the Ethogram

We developed a comprehensive ethogram of stalk-eyed fly behaviors (Table 1) by observing 20 h of flies responding to the presence of a predator and other non-predator insect stimuli. The behavioral repertoire included in the ethogram consists solely of actions that were directed at the predator during aggressive interactions; non-predatory insects failed to elicit a similar behavioral response. Behaviors include: groom, abdomen bob, approach, display, jab, flight, retreat, and escape (Table 1, Fig. 1). Groom is considered a non-aggressive behavior, abdomen bob and approach are moderately aggressive, and display and jab are highly aggressive. In addition to these fly behaviors, spider behaviors that resulted in direct interaction with the fly (spider retreat, pounce, catch, and death) were also included in the ethogram to allow us to analyze spider actions to ensure that the differences observed in fly behavior were not confounded by the actions of the predator. All behaviors included are mutually exclusive and exhaustive.

Table 1: Ethogram of behaviors scored during predation interactions between *Teleopsis dalmanni* and *Phidippus audax*

Behavior	Description
Fly actions	
Groom	Rubs front tarsi together or uses them to stroke the eyestalks from head to tip; rubs back tarsi together or uses them to stroke the wings
Abdomen bob	Moves abdomen up and down at high frequency
Approach	Walks toward the spider with eyestalks parallel
Display	Raised on hind legs with forelegs spread wide in air making large sweeping circles
Jab	Uses forelegs to jab body of predator
Flight	Initiates flight
Retreat	Quickly walks away from the spider's immediate presence
Escape	Escapes spider's grasp after being caught
Death	Spider consumed fly
Spider actions	
Spider retreat	Retreats from the approaching fly
Pounce	Attempts to attack the fly
Catch	Maintains fly in its grasp after pouncing
End of encounter	Encounter ends because of separation of spider and fly

Experimental Techniques

We individually matched randomly selected, mature stalk-eyed flies of either sex with an arachnid predator. In preparation for an interaction, we standardized predator hunger by sating each spider on crickets and then depriving it of food for 7 d (Nelson & Jackson 2006). This extended starvation period ensured that the spider would immediately pursue the fly with which it was paired (Nelson et al. 2005). Prior to the interaction, we anesthetized each spider using CO_2, placed it on its ventral side under a dissection microscope at 15–20× magnification and photographed it using a digital camera. Spider size was standardized using carapace width (2.50–3.50 mm). Each predator was used in a single interaction and had no prior experiences with stalk-eyed flies.

Similarly, we photographed each anesthetized fly while lying on its thoracic spines under a dissection microscope at 15–20×. From the digital images, we measured eyestalk length, thorax width, and total body length to the nearest 0.01 mm (Wilkinson 1993) using Scion Image (National Institute of Health).

We placed subjects in a white-painted wooden arena (10 × 5 × 5 cm) lined using cotton and moist blotting paper; the forward facing wall and removable top were composed of glass to allow for filming. The arena was large enough to allow for flight and temporary escape, but small enough to force mutual awareness and repeated encounters between the fly and predator. This small space likely increased predation rates beyond those in the wild by limiting the stalk-eyed flies' normal escape response of flight; however, the interaction chamber allowed for detailed video of behavior that would be otherwise impossible in a large mesocosm. For every interaction, we positioned the spider and stalk-eyed fly on opposite sides of the arena, separated them by a metal partition, and placed the arena in an undisturbed climate-controlled room. After 24 h of acclimatization and recovery from CO_2 anesthesia, a 25-watt bulb lighted the arena from above and a Canon ZR500 handheld digital camcorder filmed

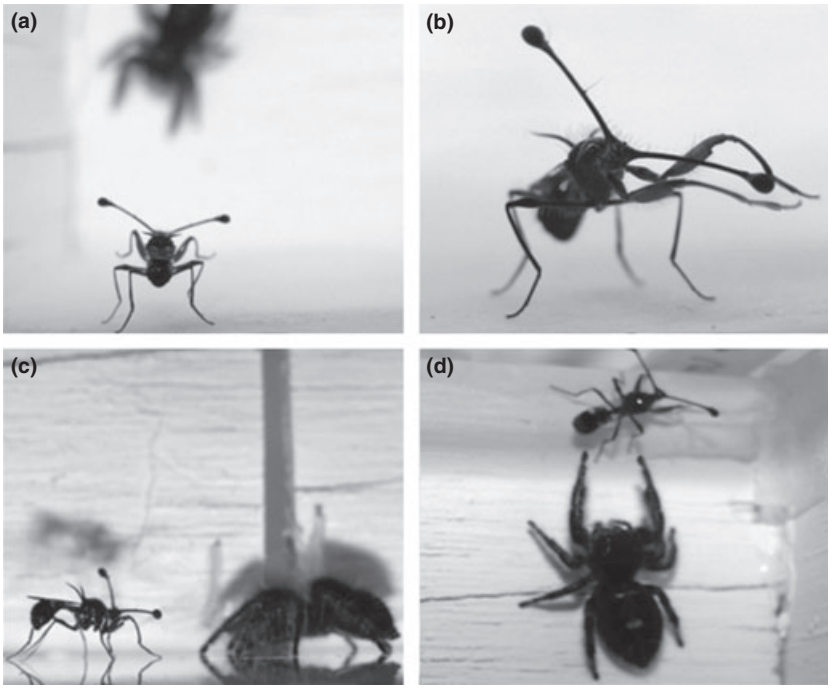


Fig. 1: Pictorial representation of fly behaviors in experimental chamber. (a) 'Display,' a high intensity behavior where the fly directs itself at the threat and rears up on its hind legs while moving its forelegs in large circles. (b) 'Groom,' when the fly uses its front tarsi to stroke and groom its eyestalks. (c) 'Approach,' fly approaches predator, typically from the side or from behind. (d) 'Pounce,' close physical contact initiated by the predator.

the interaction with the entire arena in its field of view. We removed the partition and immediately left the room, as both stalk-eyed flies and jumping spiders readily respond to human presence. The interaction was terminated after 20 min had passed. All interactions were staged from 1000 to 1400 h, which corresponded to mid-day within the laboratory light cycle. This time was chosen as it is when stalk-eyed flies are actively foraging and defending temporary territories (Burkhardt & de la Motte 1983); therefore, they are likely at an increased risk of predation by diurnal predators.

Analysis of Behaviors

A single trained observer analyzed the videotapes using the free event recorder JWatcher (Blumstein et al. 2006). Multiple encounters occurred within each trial, beginning when the fly approached and began displaying behaviors directly toward the predator, or when the predator stalked and/or attacked the stalk-eyed fly, thereby eliciting a behavioral response in return. The end of an encounter was defined by a spatial separation of the spider and fly with a 5-s lull in behavior and/or no ensuing pursuit. The onset of a behavior was scored in sequence without regard to duration, resulting in event-based data. Scoring was terminated when the 20-min interaction was complete or when the predator successfully captured the stalk-eyed fly.

Sequential analysis relying on single-order Markov chains was used to test for the existence of temporal structures in behavioral patterns that occur non-randomly. These analyses provide simple and transitional probability matrices to determine whether transitions between two behaviors are significantly different than expected if the behaviors are independent. Behavioral transition refers to the preceding–following relationship of two exclusive behaviors; for example, the transition jab–spider retreat is a sequence where jabbing behavior by the stalk-eyed fly is followed by retreat behavior of the spider. Adjusted residuals (z-scores $\pm$ 1.96) and corresponding p values ($\alpha = 0.05$) for each transition were used to determine the sequential dependence of two behaviors (Bakeman & Gottman 1997). Uncorrected z-scores at a 0.05 α-level provide a powerful estimate of significance when used with multiple comparisons and are liberal only in cases when sample size is low (Bakeman & Gottman 1997). Hence, uncorrected z-scores should not provide inflated type I error when sample sizes are adequate as in our study (Slooten 1994).

We tested whether sex significantly influenced behavioral sequences of the stalk-eyed flies by pooling the interactions and encounters (Chen et al. 2002, Egge et al. 2011) of males and females separately. The overall pattern of anti-predator behaviors was then quantified and compared by sex. Interactions that resulted in no direct encounters between

the stalk-eyed fly and the predator (22 of 117 trials) were not included in the analysis.

Behavioral transition matrices of males and females were compared using a Pearson's chi-square test of independence (Chen et al. 2002, Egge et al. 2011) to determine whether behavioral sequence of anti-predator behaviors differed significantly between the sexes. This allowed us to determine whether stalk-eyed fly behavioral sequence is independent of gender or whether each sex has a unique strategy for dealing with threats. We then calculated the cell-wise chi-square statistic to determine which individual transitions were most influential in the differences between males and females. Cells exhibiting large chi-square statistics indicate transitions that occur more or less frequently than expected by chance and can be used to differentiate sex-biased patterns in the sequence of behaviors.

Results

We observed a total of 1032 encounters in 68 male trials and an average of 15.3 ± 11.3 (mean $\pm$ SD) encounters per trial. Additionally, we observed 401 encounters in 27 female trials and an average of 14.1 ± 9.0 encounters per trial. The number of encounters per trial did not differ between males and females ($T_{93} = -0.49$, $p = 0.6233$), and no flies contributed disproportionally to the number of encounters in any of the analyses (determined by absence of statistical outliers). Sample sizes between the sexes differed because of a shortage of females in the population at the time of sampling. Sexes differed significantly in eye span and residual eye span, but not thorax width or body length (Table 2).

The behavioral transition frequencies of males differed significantly from those of females ($\chi^2_{23} = 311.52$, $p < 0.0001$), indicating that overall behavioral sequence varies between sexes. Behaviors that proved to exert the most influence on this differenc included approach–spider retreat ($\chi^2_{23} = 43.73$), display–groom ($\chi^2_{23} = 26.96$), groom–display ($\chi^2_{23} = 25.37$), and spider retreat–display ($\chi^2_{23} = 16.78$).e An extended list of all behavioral transitions with high cell-wise chi-squared values and their frequencies in each sex is listed in Table 3.

Table 2: Mean $\pm$ SD of morphological measurements of male and female *Teleopsis dalmanni*

Measurement (mm)	♂	♀	p-Value
Eye span	7.98 ± 0.54	5.72 ± 0.16	<0.0001
Body length	6.79 ± 0.32	6.68 ± 0.23	0.1784
Thorax width	1.85 ± 0.11	1.84 ± 0.07	0.5861
Residual eye span	1.18 ± 0.04	0.86 ± 0.02	<0.0001

Table 3: A list of behavioral transitions that contributed to the significant chi-squared value between males and females ($\chi^2_{23} = 311.52$, $p < 0.0001$)

Behavioral transition	Cell-wise chi-squared	Male transitional probability (%)	Female transitional probability (%)
Approach → Spider retreat	43.73	16.02[a]	1.56
Display → Groom	26.96	13.91[a]	21.95[a]
Groom → Display	26.37	70.95[a]	72.96[a]
Retreat → Display	16.88	22.56	18.60
Display → Pounce	11.50	0.75[b]	2.30
Spider retreat → Approach	11.21	16.59[a]	5.88
Retreat → Pounce	10.38	4.61[b]	5.49[b]
Flight → Abdomen bob	8.45	67.36[a]	61.64[a]
Spider retreat → End interaction	8.23	25.81[a]	41.18[a]
Abdomen bob → Approach	8.08	16.52[a]	11.70[a]
Abdomen bob → Flight	7.84	6.41[b]	3.20
Retreat → End interaction	7.08	48.59[a]	54.88[a]
Pounce → Approach	7.04	0.73[b]	4.60
Pounce → Retreat	6.55	21.17[a]	25.29[a]
Jab → Spider retreat	6.30	45.12[a]	33.33[a]
Groom → Retreat	6.26	3.58[b]	5.56
Approach → Jab	5.94	7.27[b]	4.30[b]
Spider retreat → Abdomen bob	5.70	9.68[b]	5.88
Approach → Flight	5.69	2.95[b]	0.78[b]
Escape → Abdomen bob	5.44	11.11	33.33

[a]Behavioral transitions with significant *z*-scores (>1.96) and a transitional probability >10% according to the transitional probability matrix. These transitions are represented on the kinematic diagrams.
[b]Behavioral transitions with significant *z*-scores (>1.96) according to transitional probability matrix.

Kinematic diagrams were created to provide a visual depiction of the behavioral sequences exhibited by males and females and to highlight the sex-based differences in anti-predator behavior observed during interactions (Fig. 2). These diagrams include only those behavioral transitions that occurred at a frequency greater than 10% and exhibited significant *z*-scores (>1.96) as determined from the transitional probability matrices. Not all significant transitions are represented in the kinematic diagram because some occurred at frequencies lower than 10%, which was the arbitrary level set to include transitions to maintain relatively simple visual diagrams. Significant behaviors of low frequency not depicted in the diagram should not be interpreted as being inconsequential.

Pairwise comparisons of transitional probabilities were examined to determine whether underlying patterns in behavior existed between the sexes (Table 3).

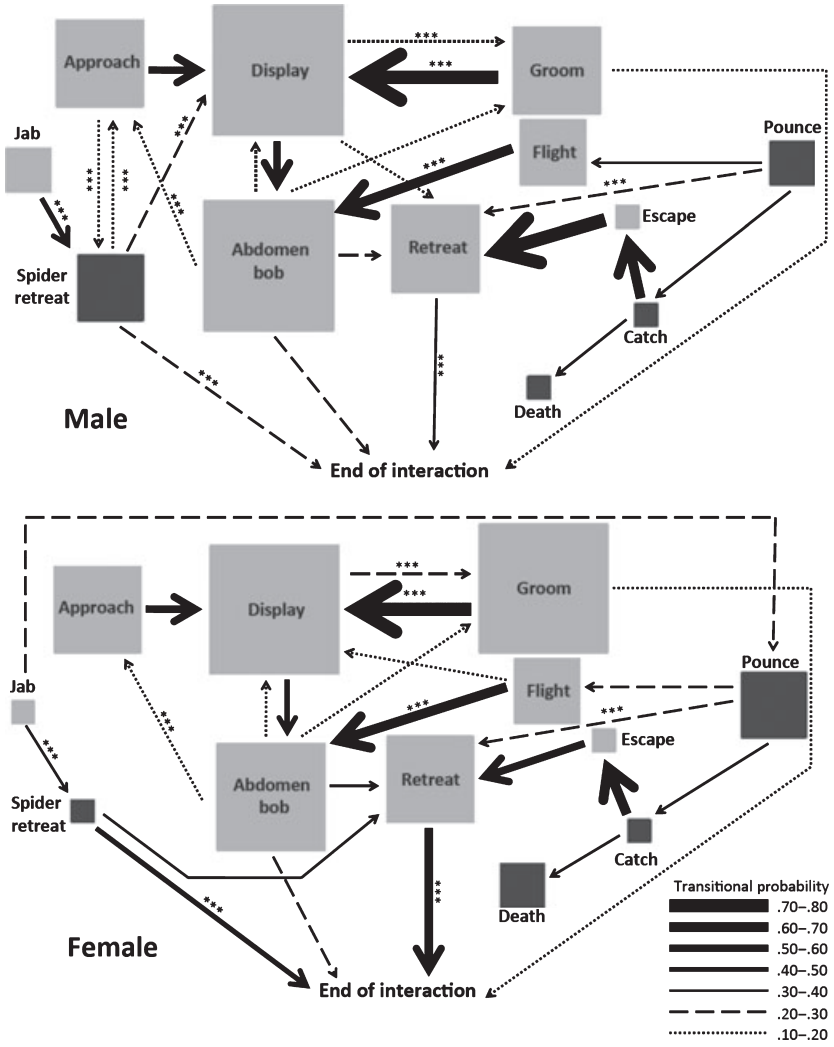


Fig. 2: Significant behavioral transitions in sequential pathway of predation encounters of male and female stalk-eyed flies. Arrow weight is proportional to the conditional probability of the transition and box size is proportional to the relative frequency of occurrence for the behavior. Light-gray boxes correspond to fly behaviors and dark-gray boxes correspond to spider behaviors. These diagrams include only those transitions that occurred at a relative frequencies >0.10 and exhibited significant *z*-scores (>1.96). Triple asterisks mark the transitions that most contributed to the difference between males and females in the chi-squared test (cell-wise $\chi^2 > 5.00$).

In all significant transitions leading to spider retreat (i.e., approach–spider retreat and jab–spider retreat), the transition occurred more often than expected by chance in males. In addition, significant transitions leading to the spider pouncing on the fly (i.e., display–pounce and retreat–pounce) occurred more than expected by chance in females. Males more frequently transitioned to increasingly aggressive behaviors toward the predator (i.e., flight–abdomen bob, abdomen bob–approach, and approach–jab), which resulted in more predator retreats than did females.

Discussion

Laboratory-reared male and female stalk-eyed flies readily interacted with an arachnid predator. Their behavioral ethograms were similar, with all behaviors observed occurring in both sexes. Display was the most frequently observed behavior after approaching the predator (males = 55.34%, females = 64.84%). Flies exhibiting this behavior rear up on their hind legs and use their most anterior pair of legs to draw large circles near the ends of their eyestalk. This potentially draws increased attention to the eyestalks, causing the predator to overestimate body size and prevent it from pursuing an attack. Display is also used agonistically between males competing for copulation sites (Burkhardt & de la Motte 1983; Panhuis & Wilkinson 1999), providing additional evidence of this behavior's importance in aggressive encounters. Transitions that included groom were also common, suggesting that eyestalk grooming could be another means of highlighting stalk length and/or body size, potentially by increasing movement near the tips of the stalks to make them more noticeable against the dense forest these flies live in. However, groom was more likely

to transition to display (males = 70.95%, females = 72.96%) than from it (males = 13.91%, females = 21.95%; Fig. 2), implying it to be a behavior interrupted by an approaching threat rather than a specific anti-predatory behavior. A more detailed examination of grooming behavior is required before conclusions can be made about its significance in aggressive encounters.

The observed frequencies of behavioral transitions exhibited by each sex did reveal differences despite the similarity in the overall behavioral repertoires. Behavioral patterns suggest that males are more aggressive toward a predator and that their aggressive actions are more likely to deter pursuit than when females exhibit those same behaviors. For example, consider transitions including approach to the spider. Males began abdomen bobbing more than females prior to predator approach (males = 16.52%, females = 11.70%). After approaching the predator, both sexes had high frequencies of display, but males were significantly more likely to physically jab the predator (males = 7.27%, females = 4.30%), leading to increased spider retreat (males = 45.12%, females = 33.33%). Additionally, by merely approaching the predator, males were over ten times more likely to cause spider retreat than were females (males = 16.02%, females = 1.56%). Even after the predator had retreated, males continued direct aggression at the spider by approach (males = 16.59%, females = 5.88% and abdomen bobbing (males = 9.68%, females = 5.88%). These trends support that when males approach a threat, either to investigate or intimidate, they are more successful at warding off predators.

Sex differences in transitions that involved pounce provided further support that females have increased predation relative to males. All significant transitions that resulted in the fly being pounced on by the spider were more frequent in females than in males. These transitions include jab–pounce (males = 9.76%, females = 25.00%), retreat–pounce (males = 2.18%, females = 5.49%), and approach–pounce (males = 3.18%, females = 7.81%). Differences in sex and behavior account for much of this difference in predation risk, where males are more effective at avoiding predation than females. In a study investigating sex differences of *T. dalmanni* in surviving predation attempts, Worthington & Swallow (2010) determined that the behavior of the predator, *P. audax*, was not significantly affected by the sex of the prey; therefore, it is unlikely that the predator's behavior account for the differences seen here.

The major morphological difference between males and females is eyestalk length. Thus, in addition to behavior, morphology may play a role in predator deterrence. In dimorphic stalk-eyed flies, the allometric relationship between eye span and body length is steeper in males than in females, resulting in greatly exaggerated male ornaments that exceed body length (Baker & Wilkinson 2001). In this study, male eye span exceeds female eye span by an average of 2 mm for flies with the same approximate body size (Table 2). As a consequence, the predator may interpret the larger male eye span as corresponding to a body larger than the male's actual size. Although *P. audax* can readily take down prey larger than themselves, larger prey cause increased caution when approaching, many times resulting in no attack (Freed 2009).

Morphology may also play a role in predator interactions because broader eye span has been shown to increase stereotypic vision (Burkhardt & de la Motte 1983). Consequently, males with larger eye spans may have greater visual abilities that allow them to monitor predator movement on a finer scale, providing a faster escape response should the predator attack. A previous study did not discover any differences in survival among males of varying eye spans, however, which would have provided support for this hypothesis (Worthington & Swallow 2010). Future work using flies standardized for eye span will elaborate on whether the difference in predation rate is due strictly to sex-based differences in anti-predator behavior or whether the eye span difference between males and females plays an important role as well. Because eye span is a condition dependent trait, larvae raised in high-density populations with limited food produce flies of similar size and small eye spans, thereby decreasing the morphological differences between males and females (Cotton et al. 2004) and allowing for more direct comparisons of the sexes not confounded by body or eyestalk size.

The behavioral differences described in this study may account for increased survival of males in the presence of a predator by reducing their overall risk of predation (Worthington & Swallow 2010). Observations of adult longevity have also been shown to positively correlate with increasing eye span within laboratory-reared populations (Wilkinson et al. 2006) and with increasing body size in field-caught flies (Wilkinson & Reillo 1994). Male stalk-eyed fly survival is greater than females in the presence of predation, suggesting there may be mechanisms present that reduce the cost of large eye span, that any associated costs present are irrelevant to

predation risk, or that increased eye span improves predator detection and avoidance. In this study, behavioral differences have been explored more in depth and likely contribute to enhanced male survival. This controlled laboratory experiment was imperative to observing and quantifying stalk-eyed fly behavior; however, future field-based predation experiments are needed to examine the effects of behavior, ornamentation, and sex on predation risk and survival in nature.

Conclusions

The analyses of behavior sequences in the context of predation provide insight into how stalk-eyed flies react to a potentially dangerous threat and how gender differences in predation-avoidance strategies affect survival. Even though males display larger ornaments that may entail reduced locomotor performance, they effectively employ behavioral strategies to mitigate predation risk. Males used aggressive actions leading to increased retreat by the predator; whereas females were less likely to engage in aggressive behaviors and elicited more direct attacks. These results demonstrate how important behavior is to survival and how it is a major factor in determining predation risk. Further studies investigating predation of stalk-eyed flies, including the use of larger mesocosms, are required to clarify the relationship of behavior, sex, and ornament size in relation to predation risk.

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