

Original Article

The degree of response to increased predation risk corresponds to male secondary sexual traits

Kasey D. Fowler-Finn and Eileen A. Hebets

Manter Hall, School of Biological Sciences, University of Nebraska, Lincoln, NE, USA

Secondary sexual traits are expected to reflect a balance between sexual selection and natural selection. We test the hypothesis that plasticity in sexual advertisement behaviors can influence this trade-off, allowing showier traits than expected for a given level of predation risk. Specifically, we tested whether the degree of behavioral plasticity exhibited in response to chemical cues of a co-occurring predatory wolf spider corresponds to courtship rate and the degree of ornamentation in male wolf spiders. Both ornamented (brush-legged) males and non-ornamented males decreased locomotion, decreased their likelihood to court, and increased their time to initiate courtship in response to predator cues. However, brush-legged males increased their time to initiate courtship more than did non-ornamented males, demonstrating a greater response to the risk of predation for the more ornamented males. Similarly, within brush-legged males, individuals with the highest courtship rates also showed the greatest degree of plasticity in time to initiate courtship across predation contexts, whereas behavioral plasticity was independent of courtship rate for non-ornamented males. We found no correlation between ornament size and plasticity in response to predator cues within brush-legged males. Ultimately, we suggest that our data provide support for the hypothesis that behavioral plasticity in response to predator cues may alter the trade-off between predation risk and sexual advertisement and may be more important for males with higher degrees of conspicuousness in ornamentation and courtship. *Key words:* antipredator behavior, behavioral plasticity, predation risk, *Schizocosa*, secondary sexual traits. [*Behav Ecol* 22:268–275 (2011)]

Male ornaments and courtship displays evolve under conflicting sources of sexual selection and natural selection. Sexual selection favors conspicuous ornamentation to increase the attraction of potential mates (Andersson 1994), whereas natural selection favors traits that are more cryptic in order to avoid detection by predators (Gadgil 1972; Cade 1975; Burk 1982; Zuk and Kolluru 1998). The expression of ornamentation should therefore reflect a balance between benefits gained via female choice and costs incurred through predation. In many systems, selection has resulted in an increase in benefits versus costs, resulting in traits that are more detectable by females than by predators. For example, the brightest colors on male crabs are on body parts not visible from the aerial perspective of avian predators (Cummings et al. 2008), and male guppy coloration is more visible during times and places of courtship versus times of highest predation (Endler 1991). Some males also exhibit facultative expression of ornamentation, such as the decreased expression of bright red nuptial coloration in sticklebacks when predation risk is high (Candolin 1998). Alternatively, males can alter the timing or frequency of signaling behaviors—field crickets call less frequently and less conspicuously when parasitoids are most abundant (Bertram et al. 2004), anolis lizards decrease the most conspicuous displays following predatory attacks (Simon 2007), and male *Pardosa* wolf spiders delay courtship and decrease copulatory behaviors when predation risk is high (Taylor et al. 2005).

Altering behaviors when predation risk is high can reduce detection and capture by predators (Downes 2001, 2002;

Persons et al. 2001; Templeton and Shriner 2004; Bell et al. 2006). However, such responses to increased predation risk often carry costs, such as reduced intake of food and water or reduced mating activities (Downes 2001; Taylor et al. 2005; Chelini et al. 2009). To minimize these costs, animals should respond to varying levels of predation risk in accordance to the perceived level of risk (Dill and Fraser 1997; Sih 1997; Puttlitz et al. 1999). Risk-dependent behavior can occur based on external cues, including the physical presence of predators or their chemical cues (lizards, Downes and Adams 2001; voles, Jedrzejewski et al. 1993; water striders, Krupa and Sih 1998; anurans, Laurila et al. 1997; spiders, Persons and Rypstra 2001; Lehmann et al. 2004). Risk-dependent behavior can also correspond to an individual's morphological features associated with predation risk. For example, in gastropods and dragonfly larvae, individuals with more predation-susceptible morphologies show greater degrees of plasticity in predator avoidance behaviors (Cotton et al. 2004; Mikolajewski and Johansson 2004).

Conspicuous ornamentation is frequently associated with increased risk of predation (Endler 1980, 1983; Godin and McDonough 2003; Stuart-Fox et al. 2003; Husak et al. 2006; Woods et al. 2007). Here, we test the hypothesis that an individual's response to predation risk is correlated with its degree of ornamentation. By more readily altering behavior in response to predation risk, more conspicuous males could maintain extravagant traits while avoiding the associated cost of predation. Such a hypothesis would predict a correlation between the response to predation risk and the degree of conspicuousness, with males possessing more conspicuous ornamentation showing a greater response to heightened predation risk. Support of this prediction has been found in field crickets, where males that are more conspicuous exhibit greater caution when threatened (Hedrick 2000). Here, we test for a relationship between conspicuousness and response to predation risk using wolf spiders with variable foreleg

Address correspondence to K.D. Fowler-Finn, who is now at University of Wisconsin, Milwaukee, Department of Biological Sciences, Lapham Hall, 3209 N Maryland Avenue Milwaukee, WI 53211, USA. E-mail: kaseyff@uwm.edu.

Received 22 July 2010; revised 8 November 2010; accepted 9 November 2010.

ornamentation and courtship behavior. We use the change in behavior in the absence versus presence of predator cues as a measure of male response.

Brush-legged and non-ornamented *Schizocosa* males are syntopic in a northern Mississippi population, where they overlap in time and space, thus sharing potential predators. However, they differ dramatically in their ornamentation and courtship: Brush-legged (sensu *S. ocreata*) males have large black brushes on their forelegs and a highly active courtship display involving body bounces, leg arches, and jerky legs taps in association with a unique vibratory display (Stratton and Uetz 1981; Stratton 1983). In contrast, non-ornamented (sensu *S. rovnerei*) males lack any foreleg ornamentation and have a more stationary courtship display that consists of a body bounce associated with a unique, and typically louder, vibratory signal (Stratton and Uetz 1981; Stratton 1983). These spiders are indistinguishable from *S. ocreata* (brush-legged) and *S. rovnerei* (non-ornamented) from the Ohio Valley, where behavioral isolation has been demonstrated based on female discrimination between potential mates (Stratton and Uetz 1981). Prior studies have also demonstrated that male *S. ocreata* and *S. rovnerei* from the Ohio Valley court conspecific and heterospecific females and female silk indiscriminately (Stratton 1983; Roberts and Uetz 2005), and both males' phenotypes from the mixed Mississippi population initiate courtship equally to females from brush-legged versus non-ornamented fathers (Sullivan-Beckers L, unpublished data). Though the precise taxonomic status of the brush-legged and non-ornamented males in the Mississippi population (the focus of this study) is unclear, behavioral and mitochondrial data suggest that they form an interbreeding population (Hebets and Vink 2007), and no genetic differentiation has been detected between them (Fowler-Finn 2009). We therefore subsequently refer to males from the mixed Mississippi population as brush-legged and non-ornamented morphs.

Brush-legged *S. ocreata* males have previously been shown to be more visually attractive to females of *S. ocreata* and *S. rovnerei* (McClintock and Uetz 1996; Scheffer et al. 1996; Uetz and Roberts 2002), while at the same time experiencing higher predation risk (i.e., increased orientations and attack rates using video playback; Pruden and Uetz 2004; Roberts et al. 2007; Roberts and Uetz 2008). This increased risk for brush-legged males emerges when brushes are coupled with active courtship displays (Pruden and Uetz 2004). Similarly, live brush-legged males from the mixed Mississippi population have also been shown to be the recipients of quicker attacks than their non-ornamented male counterparts from predators in laboratory studies allowing for visual and vibratory courtship displays (Fowler-Finn and Hebets 2011). Together, these studies demonstrate an increased predation risk associated with male foreleg brushes, yet prior studies do not speak to any potential behavioral adjustments associated with this increased risk. A separate series of studies using mostly *Pardosa* wolf spiders have found that individuals alter their behavior in response to predation risk, as manipulated via predator cues (Persons and Rypstra 2001; Persons et al. 2001, 2002; Barnes et al. 2002; Rypstra et al. 2007).

Here, using *Schizocosa* wolf spiders of 2 different morphs and building on the above-mentioned studies, we manipulate the cues that influence an individual's perceived predation risk (via the presence/absence of predator silk and excreta) and assess courtship behavior in order to test the hypothesis that an individual's response to predation risk is associated with its degree of ornamentation. By using 2 male forms that exhibit different morphologies and courtship behavior, we can test for this relationship both 1) between discrete male morphs and 2) within the male morphs—using existing variation in courtship rate as well as the degree of ornamentation.

If an individual's response to predation risk is associated with its degree of ornamentation and associated courtship behavior, then we predict that brush-legged males will show greater behavioral adjustments related to courtship between environments with predation cues absent versus present. We also predict that the degree of behavioral adjustment will correspond to courtship rate as variation in courtship rate has been shown to influence predation risk in another wolf spider (Kotiaho et al. 1998). Finally, we predict that the degree of behavioral adjustment will correspond to brush size as males with larger brushes experience quicker orientations by predators (Roberts et al. 2007; Roberts and Uetz 2008).

MATERIALS AND METHODS

We collected penultimate and antepenultimate *Schizocosa* wolf spiders on the grounds of the University of Mississippi's campus greenhouse (Lafayette Co., MS) the 19th and 20th of April 2007. We housed spiders individually and maintained them following Hebets and Vink (2007). We recorded male morph (brush-legged or non-ornamented) for all individuals on maturation. We haphazardly assigned mature males between the ages of 21 and 43 days postmaturation to a treatment (age was nonsignificant in all analyses, $P > 0.2$): predator absent (brush-legged, $N = 29$; non-ornamented, $N = 28$) or predator present (brush-legged, $N = 27$; non-ornamented, $N = 31$). We used *Hogna georgicola* wolf spiders as predators. *Hogna* are major predators of smaller wolf spiders (Persons and Rypstra 2001; Rypstra and Samu 2005), and we have observed *H. georgicola* in the field eating *Schizocosa* males on multiple occasions (Fowler-Finn KD, Hebets EA, personal observation). Movement has been shown to be important for wolf spiders to detect other individuals (Rovner 1996). Wolf spiders rely on visual cues, vibratory cues, and potentially air currents to detect other spiders (Rovner 1996; Taylor et al. 2005), and *Hogna* likely use a combination of these to detect their prey. We collected predators from the same location as the *Schizocosa* individuals and nearby sites (within 10 miles), housed them individually in the laboratory at the University of Nebraska-Lincoln, and maintained on the same 12:12 h light:dark cycle as the *Schizocosa* spiders. On arrival at the laboratory, we fed all *Hogna* 2–3 adult crickets to equalize hunger levels and subsequently fed them one adult cricket per week approximating their body size.

Experimental design

We measured male courtship behavior in the presence and absence of predator cues. Silk and excreta are naturally deposited by spiders as they move throughout the environment and are known to influence wolf spider behavior (Persons et al. 2001). Additionally, conspecific female silk cues are sufficient to elicit male courtship even when a female is absent (Roberts and Uetz 2005), and so conspecific female cues (i.e., cues from females collected from the same mixed population) were present in each environmental treatment. Although we did not know which morph the females were, we know that brush-legged and non-ornamented males do not differ in their time to initiate courtship based on female morph (Sullivan-Beckers L, unpublished data). The predator absent environmental treatment consisted of silk and excreta cues from only a conspecific female. The predator present environmental treatment consisted of silk and excreta cues from a conspecific female plus a predatory wolf spider, *H. georgicola*.

Test arenas were round plastic AMAC Plastic Products (Westbrook, ME) containers measuring 25 cm diameter with 9 cm walls, filled with 2 cm of moistened peat moss and surrounded with brown paper. Between trials, we cleaned arenas with

100% ethanol to remove all chemical cues (following Persons et al. 2001). In order to obtain conspecific female cues, we allowed an adult virgin female *Schizocosa* to remain in the test arena from 48 to 24 h prior to the trial (i.e., *Schizocosa* females deposited silk and excreta for 24 h). Predator absent arenas remained empty for the 24 h immediately preceding trials, whereas the predator present arenas were inhabited by a predatory *Hogna* for the 24 h immediately preceding the trial. This design controlled for any effects that female responses to predators have on male behavior—females laid down cues before the *Hogna* occupied the arena, and females were also not present during the trials.

We conducted trials from 13 May to 4 June 2007. During a trial, a single male was released into the center of the arena under a 2-cm diameter clear plastic vial and allowed to acclimate for 2 min before release. Trials lasted 45 min during which time an observer, blind to the experimental treatment, used a stopwatch to record the time to first movement and to quantify the time moving in the forward direction. A total of 4 observers (always blind to the treatment) participated in data collection and subsequent statistical analyses confirmed that there was no observer effect. We videotaped all trials with a Sony DVR Handycam for subsequent quantification of courtship activity.

Courtship of non-ornamented males consists of a body bounce (Uetz and Denterlein 1979; Uetz and Dondale 1979), whereas a major component of courtship of brush-legged males involves a “jerky walk” consisting of body bounces and other movements (Stratton and Uetz 1983; Delaney et al. 2007; Gibson and Uetz 2008). Despite these differences, both males exhibit body bounces as a major courtship component. Thus, in order to examine overall patterns of courtship behavior, we used body bounces to determine courtship initiation and used the number of body bounces as a proxy for courtship activity. Two independent observers, again blind to the experimental design, scored videotapes to quantify the number of body bounces for each male over the 45-min trial. To obtain courtship rate, we divided the total number of body bounces by the time from first courtship to the end of the trial. Again, subsequent statistical analyses detected no observer effect. Fitting the log-transformed data for courtship rate of all courting males to a least squares linear regression model with male morph, predation treatment and the interaction term, revealed no plasticity in courtship rate between predator treatments (least squares regression: whole model $\chi^2 = 1.3473$, degrees of freedom = 3, $P = 0.718$), a result consistent with other studies that show courtship rate is less plastic than other behaviors associated with mate acquisition (Rivero et al. 2000; Hoefler et al. 2009). Therefore, we used courtship rate as a measure of trait expression to compare with levels of plasticity in other behaviors (see within-morph comparisons).

We measured the body size for all available individuals by averaging 3 measurements of cephalothorax width measured by digital calipers. We were unable to measure all spiders because we used a subset of individuals (all from the predator cue absent trials) in a subsequent study in which the bodies were damaged (males measured for body size: $N = 45/56$ brush-legged males, $N = 43/58$ non-ornamented males). To rule out the effect of male size on behavior, we confirmed that body size did not differ between male morphs or between predator cue treatments ($P = 0.25$).

Between-morph comparison: brush-legged versus non-ornamented males

To determine if individuals alter their behavior across predation contexts and if this behavioral adjustment corresponds to discrete male ornamentation, we compared the following

behaviors between predation treatments and male morphs—likelihood to court, time to initiate courtship, time to initiate movement, and total time moving. In all statistical models, we included predator treatment and male morph as independent variables. A significant interaction term of predator treatment by male morph indicates different levels of plasticity between male morphs. To analyze time to initiate movement and time to initiate courtship, we fitted the data to parametric survival models with a Weibull distribution and were interested only in the behavior of those males that initiated movement and courtship (one non-ornamented male in the predator present treatment did not move; 34 individuals did not court—2 brush-legged and one non-ornamented male in the predator absent treatment, 12 brush-legged and 19 non-ornamented males in the predator present treatment). We used a mixed-model nominal logistic regression to analyze the factors influencing the likelihood to court. Finally, we used maximum likelihood to simulate a 2-way analysis of variance with a beta distribution in R (R Development Core Team 2005) to analyze data for time moving. Again, we were interested in only individuals who moved and so excluded individuals with a total movement time of less than 1 s during the 45-min trial (5 individuals).

All analyses other than movement time were performed in JMP (1989–2005). All means are reported as mean \pm standard error. To account for multiple comparisons (4), we used the step-up FDR method (Garcia 2004), resulting in a “modified” alpha of 0.04.

Within-morph comparisons: courtship rate

We used courtship rate as a proxy of conspicuousness that varies within each morph. We determined if the response to increased predation risk was associated with courtship rate within each morph by performing the following analysis for brush-legged and non-ornamented males separately. We fitted parametric survival models with Weibull distributions—the time to initiate courtship was the dependent variable and predator cue treatment and courtship rate were independent variables. We included the interaction term between predator cue treatment and courtship rate to test if levels of plasticity in the time to initiate courtship varied with courtship rate.

Within-morph comparisons: ornament size

We used brush size as a proxy of conspicuousness that varies within the brush-legged morph. We use this measure of ornamentation because it has been demonstrated that larger brushes increase orientations by predators (Roberts et al. 2007; Roberts and Uetz 2008). To calculate brush size, we removed and wet-mounted the right foreleg of every male (the left in 3 cases where the right was missing) in a consistent orientation using 70% ethanol and a coverslip, and on a single day took a digital photograph of each leg. We measured brush size (the total area of the brush from the lateral view) using the software program Image Pro-Discovery (Medi Cybernetics, Bethesda, MD). The average of 3 measurements per individual resulted in a single brush size score per individual. Because of damage incurred to brushes from a subsequent study, we were unable to measure all males for brush size (males measured for brush size: predator cues absent $N = 20$, predator cues present $N = 20$).

To determine how variation in the initiation of courtship corresponds to brush size, we used a standard parametric survival model fit to a Weibull distribution with brush size and courtship rate as dependent variables and time to initiate courtship as the response. We used the interaction between predator treatment and brush size as an additional variable to determine

if levels of plasticity varied with brush size. Out of necessity, we only used individuals who expressed courtship and therefore did not look at its relationship with likelihood to court.

RESULTS

Between-morph comparison: brush-legged versus non-ornamented males

Overall, both morphs decreased courtship and locomotory behavior in the predator present environment. Both morphs were less likely to court when predator cues were present, and we found no difference between the morphs either within or between predator cue treatments (Table 1; Figure 1a). Both male morphs also delayed courtship when predator cues were present; however, brush-legged males showed a greater difference in courtship delay between predator cue treatments than non-ornamented males. Although brush-legged males courted sooner than non-ornamented males in the absence of predator cues, both morphs initiated courtship at the same time when predator cues were present (Table 1; Figure 1b).

Both morphs delayed movement and decreased the total time spent moving when predator cues were present, and we found no differences between the male morphs either within or between predator cue treatments for either variable (Table 1; Figure 2).

Within-morph comparisons: courtship rate

Within brush-legged males, the relationship between courtship rate and time to initiate courtship differed between predator treatments: In the absence of predator cues, there was a negative relationship between courtship rate and time to initiate courtship, but in the presence of predator cues, courtship rate and time to initiate courtship were unrelated (Table 2; Figure 3a). Within non-ornamented males, the relationship between courtship rate and time to initiate courtship did not differ between the predator cue absent and predator cue present treatments (Table 1; Figure 3b).

Within-morph comparisons: ornament size

The relationship between brush size and likelihood to court, time to initiate movement, or time spent moving did not

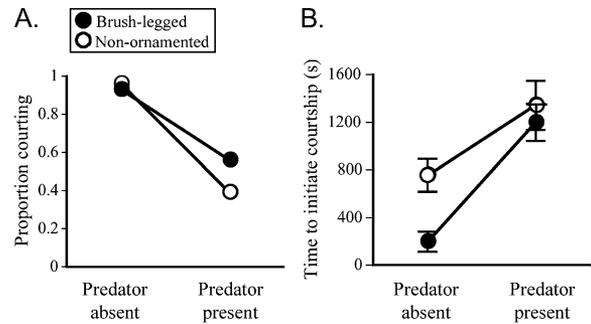


Figure 1

(A) Both male morphs were less likely to court when predator cues were present. Stars indicate significant plasticity between predator cue treatments. (Brush-legged males: predator absent $N = 27$, predator present $N = 29$; non-ornamented males: predator absent $N = 31$, predator present $N = 28$). (B) The change in time to initiate courtship between predator cue absent and predator cue present treatments was greater for brush-legged males than non-ornamented males, indicating greater behavioral plasticity for brush-legged males. When predator cues were present, both morphs initiated courtship at the same time. However, brush-legged males initiate courtship sooner when predator cues were absent (Brush-legged males: predator absent $N = 27$, predator present $N = 15$; non-ornamented males: predator absent $N = 27$, predator present $N = 11$).

change between predator cue treatments ($P > 0.3$ for all analyses). The relationship between brush size and time to initiate courtship did not differ between predator cue treatments (Table 2).

DISCUSSION

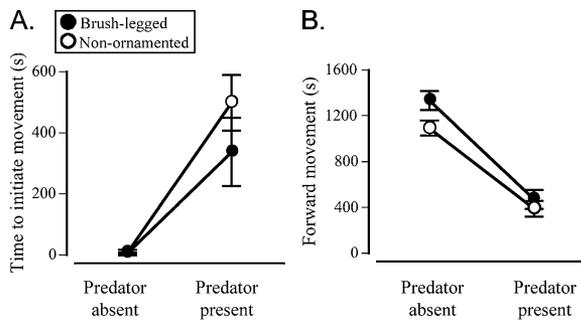
Predation has been implicated as an important influence on the evolution of male display traits (Endler 1980, 1983; Ryan and Tuttle 1982; Stuart-Fox et al. 2003; Basolo and Wagner 2004; Zuk et al. 2006). Here, we provide evidence that behavioral plasticity may enable animals to adjust the trade-off between predation risk and sexual advertisement. We demonstrate that behavioral plasticity in response to the threat of predation corresponds to variation in secondary sexual traits, though not for all traits that we measured. Studying 2 morphs of male wolf spider that differ dramatically in their secondary sexual traits and associated behavior, we found that

Table 1

Testing for differences among brush-legged and non-ornamented males in the degree of change in behaviors across predator cue environments

Behavior of interest	<i>N</i>	Factor	df	χ^2	<i>P</i>
Likelihood to court	115	Whole model	3	37.98	<0.0001
		Male morph		0.00	0.9939
		Predator cue treatment		35.1	<0.0001
		Male morph \times treatment		1.08	0.2983
Courtship initiation	81	Whole model	3	29.28	<0.0001
		Male morph		6.96	0.0080
		Predator cue treatment		19.47	<0.0001
		Male morph \times treatment		4.47	0.0351
Initiation of movement	114	Whole model	3	77.95	<0.0001
		Male morph		3.41	0.0647
		Predator cue treatment		73.59	<0.0001
		Male morph \times treatment		0.15	0.6965
Time moving	110	Whole model	3	74.57	<0.0001
		Male morph		1.79	0.1812
		Predator cue treatment		71.71	<0.0001
		Male morph \times treatment		1.93	0.1630

Significant *P* values are shown in bold. df, degrees of freedom.

**Figure 2**

Both male morphs (A) delayed first movement time (Brush-legged males: predator absent $N = 29$, predator present $N = 27$; non-ornamented males: predator absent $N = 27$, predator present $N = 30$) and (B) decreased total movement time when predator cues were present (Brush-legged males: predator absent $N = 27$, predator present $N = 27$; non-ornamented males: predator absent $N = 28$, predator present $N = 27$).

brush-legged and non-ornamented males decreased courtship and locomotory behaviors when exposed to predator cues. Importantly, the more visually conspicuous brush-legged males showed a greater degree of behavioral plasticity—adjusting their time to initiate courtship to a greater degree than non-ornamented males in response to the presence/absence of predator cues. Also, within morphs, variation in male courtship rate corresponded with the degree of behavioral plasticity for time to initiate courtship but only for courtship rate and only within the more ornamented brush-legged males. The greater the rate of courtship, the more brush-legged males adjusted the time to initiate courtship in response to the presence/absence of predator cues. Below, we discuss these results and argue for the importance of behavioral plasticity in mediating the trade-off between natural and sexual selection.

We predicted that males would exhibit behavioral plasticity in response to the degree of predation risk in the environment, as measured by the presence/absence of predator cues. Brush-legged and non-ornamented males adjusted their behavior according to their perceived risk of predation, taking longer to initiate courtship, being less likely to engage in courtship, taking longer to initiate movement, and spending less time moving when predator cues were present. These results are in

line with a series of results from other wolf spider species, where prey spiders alter their behavior in the presence of predator cues (Persons et al. 2001, 2002; Taylor et al. 2005). An individual's ability to respond behaviorally to high risk of predation has been shown to enhance survival in spiders and other taxa (lizards, Downes 2002; spiders, Persons et al. 2002), thus we expect that the plasticity exhibited here by brush-legged and non-ornamented males similarly leads to increased survivorship when predation risk is high.

When comparing the degree of behavioral plasticity between morphs, we found that the more visually conspicuous brush-legged morph, which is also at higher risk of predation (see Fowler-Finn and Hebets 2011; Pruden and Uetz 2004; Roberts et al. 2007; Roberts and Uetz 2008), demonstrated a greater degree of behavioral plasticity across predation contexts. This greater degree of behavioral plasticity can be seen when comparing the change in time to initiate courtship for each morph in the absence versus presence of predator cues. Though the time to initiate courtship was the same for both morphs when predator cues were present, brush-legged males show a greater increase in the time to initiate courtship, therefore demonstrating greater behavioral plasticity. Unfortunately, our data cannot directly speak to how this observed greater plasticity would translate into increased survival. Given that both morphs initiate courtship at the same time in the presence of predator cues (Figure 1b), a direct link between greater behavioral plasticity and increased survival is not straightforward. Nonetheless, brush-legged males clearly adjust their courtship behavior in response to predator cues more than do non-ornamented males. Two species of rock lizard demonstrate a similar pattern, with one species demonstrating a greater response to predation risk that may help sustain its correspondingly more conspicuous coloration (Cabido et al. 2009).

Brush-legged males from this population are known to be more sexually aggressive (Hebets and Vink 2007), so it may not be surprising that these males initiated courtship more quickly than non-ornamented males in the absence of predator cues. This early courtship by brush-legged males could result in an additional mating advantage; in prior studies with *S. ocreata*, when given the choice between 2 males, females mated more frequently with the first male to initiate courtship (Scheffer et al. 1996). Regardless of why brush-legged males court sooner in the absence of predator cues, their greater plasticity may lower their risk of predation associated with

Table 2

Parametric survival models testing within morph for whether the change in time to initiate courtship across predator cue treatments corresponds to variation in courtship rate and ornament size

Trait of interest	N	Factor	df	χ^2	P
Courtship rate—brush-legged and non-ornamented males					
Brush-legged males	41	Whole model	3	25.06	<0.0001
		Courtship rate		3.56	0.0591
		Predator cue treatment		18.96	<0.0001
Non-ornamented males	38	Courtship rate \times Treatment		5.43	0.0197
		Whole model	3	3.92	0.2701
		Courtship rate		0.22	0.6408
		Predator cue treatment		3.25	0.0713
		Courtship rate \times Treatment		0.05	0.8217
Ornament size—brush-legged males					
Brush size	40	Whole model	3	11.81	0.0081
		Brush size		0.03	0.8653
		Predator cue treatment		9.03	0.0027
		Brush size \times Treatment		3.32	0.0686

Significant P values are shown in bold. df, degrees of freedom.

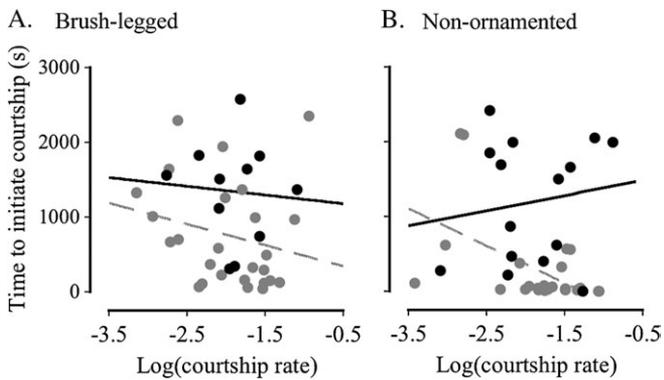


Figure 3

Time to initiate courtship as it relates to courtship rate when predator cues are absent (gray circles) and predator cues are present (black circles). Axes are the same for panels (A) and (B). (A) Brush-legged males with higher rates of courtship initiated courtship sooner in the absence of predator cues ($N = 26$) but initiated courtship later in the presence of predator cues ($N = 15$). (B) For non-ornamented males, the relationship between courtship rate and time to initiate courtship did not differ between predator treatments (predator cues absent $N = 27$, predator cues present $N = 11$).

courtship. Further studies are necessary to fully understand the relationship between time to initiate courtship, survival, and mating success for brush-legged versus non-ornamented males.

We found support for our prediction that the degree of behavioral plasticity correlates with the rate of courtship within a male morph. The higher the rate of courtship, the greater a brush-legged male adjusts its time to initiate courtship based on the presence/absence of predator cues. Male spiders and fireflies with higher display rates suffer elevated predation (spiders, Kotiaho et al. 1998; Lindstrom et al. 2006; fireflies, Woods et al. 2007). The greater behavioral plasticity we observed for brush-legged males with higher courtship rates may offset increased predation costs associated with high display rates. Similar results were found in a field cricket, where males with calls that are more conspicuous show greater caution after a disturbance (Hedrick 2000). It is important to note that non-ornamented males with higher display rates did not adjust the time to initiate courtship across predation contexts. However, visual conspicuousness, or the combination of visual and vibratory traits, may be the major concern for attracting predators, and the courtship display of non-ornamented males is considered mostly vibratory (Uetz and Denterlein 1979; Uetz and Dondale 1979). Previous studies assessing risk and ornamentation have shown greater risk as a result of the combination of courtship and ornamentation (Pruden and Uetz 2004; Roberts et al. 2007), and so the combination of brushes and active courtship for brush-legged males may necessitate greater behavioral compensation to decrease predation costs.

Within brush-legged males, we found no support for a relationship between ornament size and the degree of behavioral plasticity in any behavior examined. First, once a male has brushes, variation in the size of the brush may not significantly influence the attraction of predators (but see Roberts et al. 2007; Roberts and Uetz 2008). Second, brush-legged males are more sexually aggressive than non-ornamented males (Hebets and Vink 2007). A correlation between aggression and risky behavior (as seen in many taxa: fish, Bell 2005; spiders, Johnson and Sih 2007; crickets, Kortet and Hedrick 2007; spiders, Riechert and Hedrick 1993) could help explain the low risk aversion in the presence of predator cues of males with large brushes. Additionally, condition-dependent expres-

sion of brushes (demonstrated in *S. ocreata*, Uetz et al. 2002) may influence the relationship between ornamentation, behavioral plasticity, and survival. Previous studies on other spiders have demonstrated positive relationships between male condition, trait expression, and survival (Kotiaho et al. 1999; Kotiaho 2000; Hoefler et al. 2008). These findings are consistent with those from numerous other taxonomic groups in which males with greater expression of secondary sexual traits showed greater survival, a pattern frequently suggested to result from condition-dependent trait expression (see review: Jennions et al. 2001). Although brush-legged males show increased escapes to predator attacks as compared with non-ornamented males (Fowler-Finn and Hebets 2011), the relationship between predator evasion and condition-dependent trait expression has not been examined in *Schizocosa* wolf spiders. We would expect that such a relationship would alter the expectations for the interplay between trait expression and adaptive behavioral plasticity in response to elevated predation risk.

Here, we present evidence that adaptive behavioral plasticity can potentially offset or resolve trade-offs between the costs and benefits of sexually selected traits. The plasticity in behavioral responses to predation risk that we observed suggests that males can minimize predation costs by shifting their behavior patterns across levels of predation risk. We found that the degree of behavioral plasticity depended on discrete variation in ornamentation, as well as continuous variation in courtship rates. More ornamented males (brush-legged) showed greater plasticity when compared with their non-ornamented counterparts. Additionally, plasticity corresponded to courtship rate only within the more ornamented (brush-legged) males. Greater plasticity by more ornamented males suggests that behavioral plasticity that minimizes predation risk associated with secondary sexual traits may be more important in taxa with more conspicuous traits. Ultimately, plasticity in sexual advertisement behavior in responses to the risk of predation can provide a mechanism whereby conspicuous secondary sexual traits are sustained by altering the trade-off between natural selection by predators and sexual selection for conspicuous traits.

FUNDING

Monetary support was provided by a National Science Foundation Graduate Fellowship to K.D.F.F. and an Initiative for Ecological and Evolutionary Analysis Research Grant In-Aid-Of, School of Biological Sciences, University of Nebraska to K.D.F.F.

Many thanks to people who helped collect the spiders: Aaron Rundus, Gail Stratton, and Pat Miller, and the University of Mississippi greenhouse staff for allowing collection. Dustin Franklin helped with spider care and weighing individuals. Katie Swoboda, Dustin Franklin, and Bronson Boosalis helped conduct predator cue trials. Chad Brassil and Bill Wagner gave invaluable statistical advice, Reed Stubbendeick and Mari Pesek scored videotapes for courtship behavior, and Mari Pesek measured body sizes. This manuscript was greatly improved by thoughtful comments from Rafael Rodríguez, Bill Wagner, Alex Basolo, Chandreyee Mitra, Dustin Wilgers, Oliver Beckers, Laura Sullivan Beckers, Mitch Bern, Matt Adams, Cassie Martin, Ashley Bowers, Jay Storz, Darren Rebar, Gil Rosenthal, and 2 anonymous reviewers.

REFERENCES

- Andersson M. 1994. Sexual selection. Princeton (NJ): Princeton University Press.
- Barnes MC, Persons MH, Rypstra AL. 2002. The effect of predator chemical cue age on antipredator behavior in the wolf spider *Paradisa milvina* (Araneae: Lycosidae). *J Insect Behav*. 15:269–281.
- Basolo AL, Wagner WE. 2004. Covariation between predation risk, body size and fin elaboration in the green swordtail, *Xiphophorus helleri*. *Biol J Linn Soc*. 83:87–100.

- Bell AM. 2005. Behavioral differences between individuals and two populations of stickleback (*Gasterosteus aculeatus*). *J Evol Biol.* 18:464–473.
- Bell RD, Rypstra AL, Persons MH. 2006. The effect of predator hunger on chemically mediated antipredator responses and survival in the wolf spider *Pardosa milvina* (Araneae: Lycosidae). *Ethology.* 112:903–910.
- Bertram SM, Orozco SX, Bellani R. 2004. Temporal shifts in conspicuousness: mate attraction displays of the texas field cricket, *Gryllus texensis*. *Ethology.* 110:963–975.
- Burk T. 1982. Evolutionary significance of predation on sexually signalling males. *Fla Entomol.* 65:90–104.
- Cabido C, Galan P, Lopez P, Martin J. 2009. Conspicuousness-dependent antipredatory behavior may counteract coloration differences in Iberian rock lizards. *Behav Ecol.* 20:362–370.
- Cade W. 1975. Acoustically orienting parasitoids: fly phonotaxis to cricket song. *Science.* 190:1312–1313.
- Candolin U. 1998. Reproduction under predation risk and the trade-off between current and future reproduction in the threespine stickleback. *Proc R Soc Lond B Biol Sci.* 265:1171–1175.
- Chelini MC, Willemart RH, Hebets EA. 2009. Costs and benefits of freezing behavior in the harvestman *Eumesosoma roeweri* (Arachnida, Opiliones). *Behav Processes.* 82:153–159.
- Cotton PA, Rundle SD, Smith KE. 2004. Trait compensation in marine gastropods: shell shape, avoidance behavior, and susceptibility to predation. *Ecology.* 85:1581–1584.
- Cummings ME, Jordao JM, Cronin TW, Oliveira RF. 2008. Visual ecology of the fiddler crab, *Uca tangeri*: effects of sex, viewer and background on conspicuousness. *Anim Behav.* 75:175–188.
- Delaney KJ, Roberts JA, Uetz GW. 2007. Male signaling behavior and sexual selection in a wolf spider (Araneae: Lycosidae): a test for dual functions. *Behav Ecol Sociobiol.* 62:67–75.
- Dill LM, Fraser AHG. 1997. The worm re-turns: hiding behavior of a tube-dwelling marine polychaete, *Serpula vermicularis*. *Behav Ecol.* 8:186–193.
- Downes S. 2001. Trading heat and food for safety: costs of predator avoidance in a lizard. *Ecology.* 82:2870–2881.
- Downes SJ. 2002. Does responsiveness to predator scents affect lizard survivorship? *Behav Ecol Sociobiol.* 52:38–42.
- Downes SJ, Adams M. 2001. Geographic variation in antsnake tactics: the evolution of scent-mediated behavior in a lizard. *Evolution.* 55:605–615.
- Endler JA. 1980. Natural selection on color patterns in *Poecilia reticulata*. *Evolution.* 34:76–91.
- Endler JA. 1983. Natural and sexual selection on color patterns in poeciliid fishes. *Environ Biol Fishes.* 9:173–190.
- Endler JA. 1991. Variation in the appearance of guppy color patterns to guppies and their predators under different visual conditions. *Vision Res.* 31:587–608.
- Fowler-Finn KD. 2009. Exploring the maintenance of and selection on two distinct male morphs in a *Schizocosa* wolf spider [PhD dissertation]. Lincoln (NE): University of Nebraska.
- Fowler-Finn KD, Hebets EA. Forthcoming 2011. More ornamented males exhibit increased predation risk and antipredator behavior, but not greater mortality. *Ethology.*
- Gadgil M. 1972. Male dimorphism as a consequence of sexual selection. *Am Nat.* 106:574–580.
- Garcia LV. 2004. Escaping the Bonferroni iron claw in ecological studies. *Oikos.* 105:657–663.
- Gibson JS, Uetz GW. 2008. Seismic communication and mate choice in wolf spiders: components of male seismic signals and mating success. *Anim Behav.* 75:1253–1262.
- Godin JGJ, McDonough HE. 2003. Predator preference for brightly colored males in the guppy: a viability cost for a sexually selected trait. *Behav Ecol.* 14:194–200.
- Hebets EA, Vink CJ. 2007. Experience leads to preference: experienced females prefer brush-legged males in a population of syntopic wolf spiders. *Behav Ecol.* 18:765–771.
- Hedrick AV. 2000. Crickets with extravagant mating songs compensate for predation risk with extra caution. *Proc R Soc Lond B Biol Sci.* 267:671–675.
- Hoefler CD, Carlasio AL, Persons MH, Rypstra AL. 2009. Male courtship repeatability and potential indirect genetic benefits in a wolf spider. *Anim Behav.* 78:183–188.
- Hoefler CD, Persons MH, Rypstra AL. 2008. Evolutionarily costly courtship displays in a wolf spider: a test of viability indicator theory. *Behav Ecol.* 19:974–979.
- Husak JF, Macedonia JM, Fox SF, Saucedo RC. 2006. Predation cost of conspicuous male coloration in collared lizards (*Crotaphytus collaris*): an experimental test using clay-covered model lizards. *Ethology.* 112:572–580.
- Jedrzejewski W, Rychlik L, Jedrzejewska B. 1993. Responses of bank voles to odors of 7 species of predators: experimental data and their relevance to natural predator-vole relationships. *Oikos.* 68:251–257.
- Jennions MD, Moller AP, Petrie M. 2001. Sexually selected traits and adult survival: a meta-analysis. *Q Rev Biol.* 76:3–36.
- JMP, Version 6.0. 1989–2005. Cary (NC): SAS Institute Inc.
- Johnson JC, Sih A. 2007. Fear, food, sex and parental care: a syndrome of boldness in the fishing spider, *Dolomedes triton*. *Anim Behav.* 74:1131–1138.
- Kortet R, Hedrick A. 2007. A behavioral syndrome in the field cricket *Gryllus integer*: intrasexual aggression is correlated with activity in a novel environment. *Biol J Linn Soc.* 91:475–482.
- Kotiaho J, Alatalo RV, Mappes J, Parri S, Rivero A. 1998. Male mating success and risk of predation in a wolf spider: a balance between sexual and natural selection? *J Anim Ecol.* 67:287–291.
- Kotiaho JS. 2000. Testing the assumptions of conditional handicap theory: costs and condition dependence of a sexually selected trait. *Behav Ecol Sociobiol.* 48:188–194.
- Kotiaho JS, Alatalo RV, Mappes J, Parri S. 1999. Sexual signalling and viability in a wolf spider (*Hygalycosa rubrofasciata*): measurements under laboratory and field conditions. *Behav Ecol Sociobiol.* 46:123–128.
- Krupa JJ, Sih A. 1998. Fishing spiders, green sunfish, and a stream-dwelling water strider: male–female conflict and prey responses to single versus multiple predator environments. *Oecologia.* 117:258–265.
- Laurila A, Kujasalo J, Ranta E. 1997. Different antipredator behavior in two anuran tadpoles: effects of predator diet. *Behav Ecol Sociobiol.* 40:329–336.
- Lehmann LM, Walker SE, Persons MH. 2004. The influence of predator sex on chemically mediated antipredator response in the wolf spider *Pardosa milvina* (Araneae: Lycosidae). *Ethology.* 110:323–339.
- Lindstrom L, Ahtiainen JJ, Mappes J, Kotiaho JS, Lyytinen A, Alatalo RV. 2006. Negatively condition dependent predation cost of a positively condition dependent sexual signalling. *J Evol Biol.* 19:649–656.
- McClintock WJ, Uetz GW. 1996. Female choice and pre-existing bias: visual cues during courtship in two *Schizocosa* wolf spiders (Araneae: Lycosidae). *Anim Behav.* 52:167–181.
- Mikolajewski DJ, Johansson F. 2004. Morphological and behavioral defenses in dragonfly larvae: trait compensation and cospecialization. *Behav Ecol.* 15:614–620.
- Persons MH, Rypstra AL. 2001. Wolf spiders show graded antipredator behavior in the presence of chemical cues from different sized predators. *J Chem Ecol.* 27:2493–2504.
- Persons MH, Walker SE, Rypstra AL. 2002. Fitness costs and benefits of antipredator behavior mediated by chemotactile cues in the wolf spider *Pardosa milvina* (Araneae: Lycosidae). *Behav Ecol.* 13:386–392.
- Persons MH, Walker SE, Rypstra AL, Marshall SD. 2001. Wolf spider predator avoidance tactics and survival in the presence of diet-associated predator cues (Araneae: Lycosidae). *Anim Behav.* 61:43–51.
- Pruden AJ, Uetz GW. 2004. Assessment of potential predation costs of male decoration and courtship display in wolf spiders using video digitization and playback. *J Insect Behav.* 17:67–80.
- Puttlitz MH, Chivers DP, Kiesecker JM, Blaustein AR. 1999. Threat-sensitive predator avoidance by larval pacific treefrogs (Amphibia, Hylidae). *Ethology.* 105:449–456.
- Riechert SE, Hedrick AV. 1993. A test for correlations among fitness-linked behavioral traits in the spider *Agenlenopsis-aperta* (Araneae, Agelenidae). *Anim Behav.* 46:669–675.
- Rivero A, Alatalo RV, Kotiaho JS, Mappes J, Parri S. 2000. Acoustic signalling in a wolf spider: can signal characteristics predict male quality? *Anim Behav.* 60:187–194.
- Roberts JA, Taylor PW, Uetz GW. 2007. Consequences of complex signaling: predator detection of multimodal cues. *Behav Ecol.* 18:236–240.
- Roberts JA, Uetz GW. 2005. Information content of female chemical signals in the wolf spider, *Schizocosa ocreata*: male discrimination of reproductive state and receptivity. *Anim Behav.* 70:217–223.

- Roberts JA, Uetz GW. 2008. Discrimination of variation in a male signaling trait affects detection time in visual predators. *Ethology*. 114:557–563.
- Rovner JS. 1996. Conspecific interactions in the lycosid spider *Rabidosia rabida*: the roles of different senses. *J Arachnol*. 24:16–23.
- Ryan MJ, Tuttle MD. 1982. Bat predation and sexual advertisement in a neotropical anuran. *Am Nat*. 119:136–139.
- Rypstra AL, Samu F. 2005. Size dependent intraguild predation and cannibalism in coexisting wolf spiders (Araneae, Lycosidae). *J Arachnol*. 33:390–397.
- Rypstra AL, Schmidt JM, Reif BD, DeVito J, Persons MH. 2007. Tradeoffs involved in site selection and foraging in a wolf spider: effects of substrate structure and predation risk. *Oikos*. 116:853–863.
- Scheffer SJ, Uetz GW, Stratton GE. 1996. Sexual selection, male morphology, and the efficacy of courtship signalling in two wolf spiders (Araneae: Lycosidae). *Behav Ecol Sociobiol*. 38:17–23.
- Sih A. 1997. To hide or not to hide? Refuge use in a fluctuating environment. *Trends Ecol Evol*. 12:375–376.
- Simon VB. 2007. Not all signals are equal: male brown anole lizards (*Anolis sagrei*) selectively decrease pushup frequency following a simulated predatory attack. *Ethology*. 113:793–801.
- Stratton GE. 1983. Comparison of courtship behaviors and interspecific crosses in the *Schizocosa ocreata* species complex (Araneae, Lycosidae). *Am Zool*. 57:865–872.
- Stratton GE, Uetz GW. 1981. Acoustic communication and reproductive isolation in two species of wolf spiders (Araneae: Lycosidae). *Science*. 214:575–576.
- Stratton GE, Uetz GW. 1983. Communication via substratum-coupled stridulation and reproductive isolation in wolf spiders. *Anim Behav*. 31:164–172.
- Stuart-Fox DM, Moussalli A, Marshall NJ, Owens IPF. 2003. Conspicuous males suffer higher predation risk: visual modelling and experimental evidence from lizards. *Anim Behav*. 66:541–550.
- Taylor AR, Persons MH, Rypstra AL. 2005. The effect of perceived predation risk on male courtship and copulatory behavior in the wolf spider *Pardosa milvina* (Araneae, Lycosidae). *J Arachnol*. 33:76–81.
- Team RDC. 2005. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing.
- Templeton CN, Shriner WM. 2004. Multiple selection pressures influence Trinidadian guppy (*Poecilia reticulata*) antipredator behavior. *Behav Ecol*. 15:673–678.
- Uetz GW, Denterlein G. 1979. Courtship behavior, habitat, and reproductive isolation in *Schizocosa roovneri* Uetz and Dondale (Araneae: Lycosidae). *J Arachnol*. 7:121–128.
- Uetz GW, Dondale CD. 1979. A new wolf spider in the genus *Schizocosa* (Araneae: Lycosidae) from Illinois. *J Arachnol*. 7:86–88.
- Uetz GW, Papke R, Kilinc B. 2002. Influence of feeding regime on body size, body condition and a male secondary sexual character in *Schizocosa ocreata* wolf spiders (Araneae, Lycosidae): condition-dependence in a visual signaling trait. *J Arachnol*. 30:461–469.
- Uetz GW, Roberts JA. 2002. Multisensory cues and multimodal communication in spiders: insights from video/audio playback studies. *Brain Behav Evol*. 59:222–230.
- Woods WA, Hendrickson H, Mason J, Lewis SM. 2007. Energy and predation costs of firefly courtship signals. *Am Nat*. 170:702–708.
- Zuk M, Kolluru GR. 1998. Exploitation of sexual signals by predators and parasitoids. *Q Rev Biol*. 73:415–438.
- Zuk M, Rotenberry JT, Tinghitella RM. 2006. Silent night: adaptive disappearance of a sexual signal in a parasitized population of field crickets. *Biol Lett*. 2:521–524.