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# Detection of predator cues alters mating tactics in male wolf spiders

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## Abstract

Males of the wolf spider, *Rabidosa punctulata*, exhibit condition-dependent alternative mating tactics, whereby small, poor condition males engage in multimodal courtship while large, good condition males adopt a direct mount tactic that forgoes courtship. This study explores the possibility that tactic-specific costs can help explain this unintuitive pattern of mating tactic expression. Specifically, we hypothesize that courtship signaling is costly with respect to eavesdropping by predators and that males can alter their tactic expression based upon the perceived environmental predation risk. We test this by first examining the risk of predation associated with different mating tactics. We use a co-occurring predatory heterospecific, *R. rabida* as our predator. We found support for the prediction that courting *R. punctulata* males tended to be attacked more often than non-courting males, and the likelihood of being attacked was best predicted by courtship activity. Given this documented cost, we hypothesized that *R. punctulata* males would adjust their mating tactic based upon perceived predation risk. In a second experiment, we manipulated perceived predation risk by providing *R. punctulata* males with different female silk cues (conspecific; predatory heterospecific; conspecific + predatory heterospecific) and examined mating tactic expression. In support of our hypothesis, males were more likely to adopt the direct mount tactic in the presence of predatory heterospecific or mixed silk cues and were more likely to court in the presence of conspecific cues. These results support the hypothesis that the cost of predation from eavesdroppers may influence the evolution and expression of male alternative mating tactics in *R. punctulata*.

**Keywords:** *Rabidosa*, signaling costs, alternative mating tactic, eavesdropping, courtship plasticity

## 1. Introduction

Alternative male mating tactics are suggested to evolve as an adaptive response that maximizes individual fitness. When tactics are plastic, the expression of one over another often represents a balancing act reflecting both costs and benefits related to each mating encounter. Variation in intrinsic (e.g., body condition, age) and/or extrinsic (e.g., habitat heterogeneity, competition, predation) factors associated with each mating encounter not only directly influences the potential benefits (i.e., likelihood of mating) but also the associated costs of the interaction (Gross, 1996; Brockmann, 2001; Shuster &Wade, 2003). Given the often dichotomous nature of alternative mating tactics (e.g., signaler vs. sneaker, territorial vs. sneaker), their costs are likely to be distinct.

Courtship displays are frequently associated with increased predation risk. Courtship signals can advertise an individual's location and/or quality to potential mates (Bradbury & Vehrencamp, 1998); however, heterospecific eavesdroppers (e.g., predators or parasites) can also utilize these advertising signals to locate potential prey or hosts (Burk, 1982; Zuk & Kolluru, 1998). Across diverse taxa, this cost of predation (i.e., from eavesdropping) appears to have selected for males that can assess the presence or proximity of predators using a variety of environmental cues across (Lima & Dill, 1990), and subsequently alter their signaling behaviors in such a way that decreases their probability of detection (reviewed across taxa in Burk, 1982; Lima & Dill, 1990; Magnhagen, 1991; Reynolds, 1993; Sih, 1994). For example, upon detection of predators or perceived risk, males have been shown to alter various aspects of their courtship including: courtship intensity (Farr, 1975; Tuttle & Ryan, 1982; Luyten & Liley, 1985; Magurran & Seghers, 1990; Forsgren & Magnhagen, 1993; Reynolds et al., 1993; Candolin, 1997; Candolin & Voigt, 1998; Koga et al., 1998), courtship location (Tuttle & Ryan, 1982; Candolin & Voigt, 1998; Krupa & Sih, 1998), and signal characteristics (Tuttle & Ryan, 1982; Ryan, 1985; Hedrick, 2000). In some spiders, predatory attacks are often directed towards more conspicuous and courting males (Pruden & Uetz, 2004; Roberts et al., 2007; Hoefler et al., 2008; Fowler-Finn & Hebets, 2011a); however, more conspicuous males are known to wait longer to initiate courtship, thus decreasing their predation risk (Fowler-Finn & Hebets, 2011b).While these alterations in courtship behavior reduce predator-associated costs, males employing them often suffer a reduction in reproductive benefits due to lower mating success (Magnhagen, 1991).

One potential path to avoid reduced mating success in the face of high predation risk is to adopt an alternative mating tactic. In fact, several studies have demonstrated that males differentially use mating tactics based upon the detection of predators or perceived risk of predatory eavesdroppers (Endler, 1987; Reynolds et al., 1993; Godin, 1995; Oku & Yano, 2008); and that males adopting less conspicuous mating tactics experience lower predation risk (Cade, 1979; Howard, 1984; Larison, 2007). We explore whether predation costs associated with predatory eavesdropping heterospecifics could influence mating tactic expression in the wolf spider *Rabidosa punctulata*.

Male *R. punctulata* exhibit condition-dependent alternative mating tactics (condition as a proxy of energy reserves; Wilgers et al., 2009). When encountering a female, males adopt one of three tactics: (1) "courtship," consisting of multimodal displays involving relatively continuous vibratory signals interspersed with brief but intense visual leg waving; (2) "direct mount," consisting of a male directly mounting and briefly grappling with a female for copulation; or (3) "mixed," consisting of males using both tactics sequentially (in either order). The pattern of condition-dependent expression is intriguing as small, poor condition males predominantly utilize courtship, whereas large, good condition males typically adopt the direct mount tactic (Wilgers et al., 2009).While overall, all tactics are equally successful in terms of their benefits (i.e., males acquiring a mating), large, good condition males experience a mating advantage relative to poor condition males when using the courtship tactic (Wilgers et al., 2009), raising the question of why high condition males do not always express courtship. We propose that courtship is costly due to predatory eavesdroppers and that males can adjust their tactic expression based upon the perceived predatory environment.

Females of the predatory heterospecific, *R. rabida* have been observed to attack and kill female *R. punctulata* during interactions (Nossek & Rovner, 1983). These two species are syntopic in parts of their range, with *R. rabida* measuring approx. 47% larger in body size (Brady & McKinley, 1994). Due to their slightly offset breeding season (in Eastern NE, peak season for *R. punctulata* is approx. 6 weeks after *R. rabida*), predatory heterospecifics (*R. rabida*) are gravid and found throughout the signaling environment of *R. punctulata* males (Wilgers, pers. obs.). Feeding rates and mass of these predatory heterospecifics also directly correlate with female fecundity (Reed & Nicholas, 2008), making these gravid females likely voracious predators. Additionally, the predatory heterospecifics are sexually cannibalistic (Wilgers & Hebets, 2012) which demonstrates that females are readily able to attack and consume potentially dangerous prey much larger than *R. punctulata* (cephalothorax width; male *R. rabida* $\bar{x}$ = 6.5 ± 0.27 mm, male *R. punctulata* $\bar{x}$ = 4.6 ± 0.12 mm; Brady & McKinley, 1994).

Females of both *R. punctulata* and their predatory heterospecific (*R. rabida*) are highly dependent upon detecting vibratory courtship signals from conspecifics for mating success (Wilgers & Hebets, 2011, 2012;Wilgers, unpublished data). Due to this, females of both species are likely quite attentive to their acoustic environment. We suggest that courting *R. punctulata* males are at risk from predatory heterospecifics that can eavesdrop in on courtship signals. Previous studies on *R. punctulata* documented that those males that successfully copulated following courtship spent on average 550 s courting while males that successfully copulated following a direct mount spent less than 5 s grappling (Wilgers et al., 2009). Thus, not only can predatory heterospecifics eavesdrop in on *R. punctulata* male courtship, but they have ample time to do it as well.

We hypothesize that females of the predatory heterospecific, *R. rabida*, eavesdrop on courting *R. punctulata* males to acquire a meal and that this cost influences the expression of male mating tactic deployment. If indeed a “courtship” tactic carries with it this predation cost, we predict that males will express mating tactic plasticity — adopting a “direct mount” tactic in environments with high perceived predation risk.

## 2. Methods

### *2.1. Spider collection and housing*

We collected immature *R. punctulata* from a single site in Lancaster county, NE (40°44′57.1′′N, 96°49′3.78′′W) on 30 August–1 September 2008. We later collected already mature and mated female *R. rabida* from the same site on 14 September 2008 during the breeding season, of *R. punctulata*.

Upon collection, we housed spiders individually in plastic containers (8.4 × 8.4 × 11.0 cm) with visual barriers to prevent visual contact with conspecifics. We fed all *R. punculata* three approximately body-sized matched crickets weekly (i.e., matched to spider’s cephalothorax) and provided a constant source of moisture. All crickets were supplemented with Tetra-Min® (Blacksburg, VA, USA) fish flakes and Fluker’s® (Port Allen, LA, USA) cricket feed. To ensure female *R. rabida* (the predatory heterospecific) were motivated during mating cost trials, we fed all individuals 3 crickets every two weeks. We placed all spiders in a climate-controlled room (about 27°C) under a 15L:9D light regime. Spiders were checked every 2–3 days for molts until maturation upon which molting ceases.

### *2.2. Experiment I: Courtship tactic cost*

This experiment tested the prediction that *R. punctulata* males are more susceptible to heterospecific predation while engaged in the "courtship" mating tactic. To do this, we performed mating trials (N = 50) in semi-natural enclosures containing a virgin male–female pair of *R. punctulata* and a mature female predatory heterospecifics (*R. rabida*) that had not eaten in at least one week. The semi-natural enclosures consisted of a completely enclosed circular plastic arena (diameter = 19.4 cm, height = 22.4 cm) filled partly with peat-moss (3 cm deep) and vegetation. Forty grass stems and blades were anchored into the peat moss substrate, extending up to the top of the arena (Figure 1).

All individuals were weighed immediately prior to the trial (male *R. punctulata*: $\bar{x} = 0.147 \pm 0.004$ g; female *R. punctulata*: $\bar{x} = 0.202 \pm 0.004$ g; female

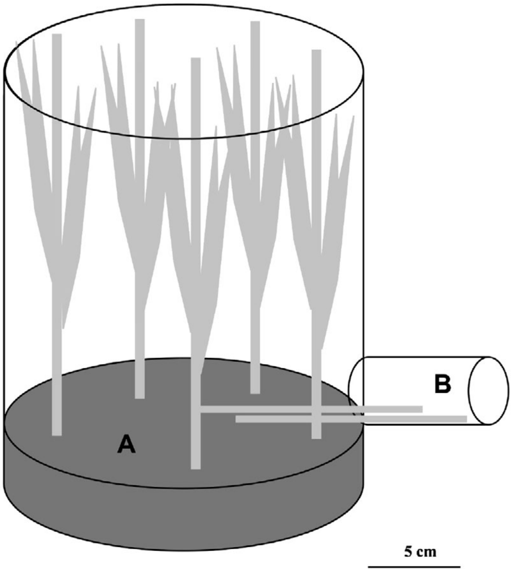

**Figure 1.** The experiment arena used to test for the predatory costs associated with courtship in male *R. punctulata*. The bottom of the arena is filled with peat moss (A), which held the grass stems in place. The compartment hooked on the side (B) was used to introduce the predator, *R. rabida*. The arena specifications are described in the paper.

predatory heterospecific: $\bar{x}$ = 0.3052 ± 0.010 g). For a given trial, a mature virgin female (12–33 days old; $\bar{x}$ = 17.9 days) was placed in the semi-natural enclosure and allowed to acclimate and deposit pheremone-laden silk for 1 h. After the acclimation period, a mature female predatory heterospecific was placed in a vial connected to an entry hole drilled into the side of the arena at the height of the peat-moss substrate. Three grass stems extended from the arena into the vial; these grass stems provided a substrate through which the mature female predatory heterospecific could potentially detect the seismic signals of a courting male (Figure 1). The predatory heterospecific's vision of the arena was initially blocked with a piece of paper. Trials began upon the introduction of the male (18–50 days old; $\bar{x}$ = 29.1 days) through the top of the enclosure. The visual barrier for the predatory heterospecific female was immediately lifted and the female was free to enter the arena. Trials lasted 45 min, during which time we recorded the following male behaviors: mating tactic (courtship, direct mount, mix), number of mounting attempts, latency to first mounting attempt, number of courtship bouts (as indicated by foreleg waves), latency to courtship(s), number of times attacked, copulation (yes/no) and latency to copulation. We also recorded the following predatory female heterospecific behaviors: latency to arena entry (s), number of male attacks, number of female attacks, number of predation events and latency to predation. In the event of copulation, the male, female, and heterospecific remained in the arena for the duration of the trial and observations continued.

All males used in this experiment had been used in one prior mating trial; each male had only been exposed to conspecific females and their silk. The males had no prior experience with female predatory heterospecifics or their silk. Arenas were cleaned with ethanol in between trials. New peat-moss and grass stems were used for each trial.

### *2.2.1. Data analysis*

During the trials one predatory heterospecific never entered the trial arena. This trial was excluded from the analysis.

In order to test for the costs of courtship in the presence of predatory heterospecifics, we used a likelihood ratio chi-square test to investigate the relationship between courting during a trial (yes: courtship or mixed tactics; no: direct mount or no tactic) and being attacked by a predatory heterospecific during a trial (yes/no). We also used a logistic regression to test whether the number of courtship bouts during a trial increased the likelihood of being attacked. Our predictor variable was number of courtship bouts and our response variable was recorded as attack or no attack (yes/no).

All analyses were performed using JMP (version 6.0, SAS Institute, Cary, NC, USA). If data failed normality, nonparametric analyses were used. Results are reported as mean ± SE.

### *2.3. Experiment II: Predation risk and mating tactic expression*

In the second experiment, we test the hypothesis that environmental cues associated with predation risk influence the expression of male mating tactics in *R. punctulata*. One potential cue consistently deposited by wolf spiders during locomotion is dragline silk (Foelix, 1996). Dragline silk is laden with pheromones, which provide males with a variety of information about the depositor (e.g., species, sex, diet, receptivity; Tietjen, 1979a; Persons et al., 2001; Roberts & Uetz, 2004, 2005) and is known to initiate male courtship (Tietjen, 1977, 1979a). In other lycosids, detection of heterospecific silk from a known intraguild predator has resulted in reductions of overall activity levels (Persons & Rypstra, 2001; Lehmann et al., 2004; Eiben & Persons, 2007), changing courtship site selection (Folz et al., 2006; Rypstra et al., 2007) and increasing latency to initiate courtship (Taylor et al., 2005). Thus, we test the prediction that male *R. punctulata* can use silk cues in the environment to assess predation risk and subsequently alter their mating tactic expression accordingly.

We conducted mating trials each with a virgin female–male pair of *R. punctulata* in different environments representing different levels of predation risk: (1) low predation, virgin conspecific *R. punctulata* female silk (LP; N = 19); (2) high predation, heterospecific *R. rabida* female silk (HP; N = 18); or (3) medium predation, both silk types combined (MP; N = 21). The abundance of predator silk in an area can be interpreted as either a greater number of predators in the area, or a longer amount of time spent in the region by a predator, both of which directly relate to predation risk.

To collect silk for each treatment, we placed females of the appropriate species on a piece of white filter paper (diameter = 18.5 cm) for 12 h. Following this, the filter paper was cut into four equal quadrants, re-assembled using tape on the underside of the filter paper, and placed into a circular plastic arena (diameter = 20.2 cm, height = 7.3 cm). For the LP and HP treatments, all four quadrants were from a single female (either *R. punctulata* or *R. rabida*). In the MP treatment, two conspecific silk quadrants were placed in an alternating pattern with two predator silk quadrants.

Both female and male *R. punctulata* were fed one small cricket approximately half their cephalothorax length prior to the silk deposition period in order to standardize hunger and motivation for the mating trials. After the trial arena floor was constructed according to the assigned treatment (see above), females were introduced under a glass vial and allowed to acclimate for 1 min prior to male introduction. For both the LP and MP treatments, the conspecific female used in the trial was the same that deposited the silk for the cues on the arena floor. Upon introduction, males were allowed to acclimate for approximately one minute prior to trial start — at which point the glass vial was lifted from the female. Trials lasted 45 min, during which time we recorded the following in real-time: mating tactic expressed (courtship, direct mount, mix), number of mounting attempts, latency to first mounting attempt, number of courtship bouts (as indicated by foreleg waves), latency to courtship (s), number of female attacks, copulation success, latency to copulation, cannibalism, and latency to cannibalism (s). In between trials, the silk-laden filter paper was discarded and the arenas were cleaned with ethanol. All individuals in the mating trials were naïve virgins and were only used once.

All individuals were weighed immediately prior to the trial. Male trial masses varied significantly across treatments (ANOVA, $F_{2,55} = 5.1$, $p = 0.009$). Tukey–Kramer post-hoc comparisons indicated males presented with predator silk (HP; $N = 18$, $\bar{x} = 0.127 \pm 0.006$ g) were significantly lighter than those with conspecific silk (LP; $N = 19$, $\bar{x} = 0.151 \pm 0.006$ g) and both silk types (MP; $N = 21$, $\bar{x} = 0.153 \pm 0.006$ g). Female trial masses were similar across silk treatments (ANOVA, $F_{2,55} = 1.4$, $p = 0.26$). Conspecific female ages ranged from 12–22 days post-maturation and were similar across all silk treatments (Kruskal–Wallis test, $\chi^2_2 = 2.44$, $p = 0.30$). Male ages ranged from 5–23 days post-maturation and were also similar across all of our silk treatments (Kruskal–Wallis test, $\chi^2_2 = 0.55$, $p = 0.76$). Predatory females (*R. rabida*) were collected mature and of unknown age.

### *2.3.1. Data analysis*

During the trials, five males did not make a tactic decision before either the end of the trial ($N = 1$) or being cannibalized ($N = 4$), and they were not evenly distributed across silk treatments (HP = 4, MP = 1; Likelihood ratio, $\chi^2_2 = 7.0$, $p = 0.03$). These males were not included in the mating tactic analysis. Males that exhibited no mating tactic before being cannibalized were only included in the probability of courtship analysis if the latency to cannibalism was longer than the mean latency to courtship across the entire experiment ($\bar{x}$ = 242.9 s), in order to ensure males enough time to decide whether or not to court. This was only the case for two males, which were both in the HP treatment. The lone male that made no decision prior to end of the trial was included in the probability of courtship.

We used likelihood ratio analyses to compare male mating tactic responses to the silk cue treatments. After comparing the LP and HP treatments, to determine whether the different behavioral responses were due to the presence of predator silk or simply the absence of conspecific *R. punctulata* silk, we compared the combined silk treatment (MP) to each of the separate silk treatments (LP and HP). To further investigate the affect of predator silk on mating tactic expression, we grouped the treatments by the presence/absence of predator silk and performed likelihood ratio chi-square tests to test for differences in mating tactic expression among the two groups.

To examine copulation success with respect to the silk cue treatment and mating tactic used, we used a logistic regression model with silk treatment, mating tactic and their interaction predicting the probability of copulation success. We did not have enough cannibalism events (N = 5) to analyze these patterns.

All analyses were performed using JMP (version 6.0, SAS Institute). If data failed normality, nonparametric analyses were used. Results are reported as mean ± SE.

## 3. Results

### *3.1. Experiment I: Mating tactic costs*

Heterospecific *R. rabida* females readily attacked *R. punctulata*, with predation attempts occurring in 78% (38/49) of trials. Often, *R. rabida* attacked *R. punctulata* more than once in a trial ($\bar{x}$ = 2.3±0.3 attacks/trial). While both sexes were attacked in 24% of the trials (12/49), overall, males were more likely to be attacked than females (males: 63%, females: 39%; Likelihood ratio, $\chi_1^2 = 5.9$, $p = 0.01$) and were attacked more often (attacks/trial) than females (males: $\bar{x}$ = 1.6 ± 0.3; females: $\bar{x}$ = 0.7 ± 0.2; $t_{96} = 3.1$, $p = 0.002$). Interestingly, in one trial, a male attempted to mount the heterospecific *R. rabida* female and was subsequently attacked. In trials with attacks, 13%

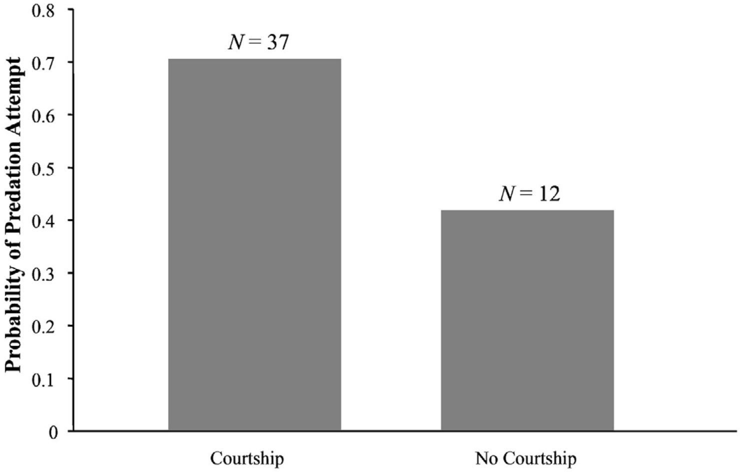

**Figure 2.** Likelihood a male was attacked by *R. rabida* during mating trials based upon courtship activity. Males that courted during trials with female *R. rabida* present were more likely to be attacked during the trial (p = 0.08).

(5/38) resulted in either death (N = 3; 2 male, 1 female) or serious injury (i.e., hemolymph or leg loss, N = 2; 1 male, 1 female).

The likelihood that a male was attacked during a trial was not influenced by his characteristics, such as mass (logistic regression, $\chi^2_1 = 0.16$, p = 0.68) or age (logistic regression, $\chi^2_1 = 0.71$, p = 0.40). Unfortunately, we had an unequal distribution of male mating tactics employed across our trials, making analysis difficult: no tactic (22.4%, N = 11/49), courtship tactic (71.4%, N = 35/49), direct mount (2%, N = 1/49), and mixed tactic (4.1%, N = 2/49). However, there were strong trends suggesting that males who courted during at trial in the presence of female *R. rabida* were more likely to be attacked (Likelihood ratio, N = 49, $\chi^2_1 = 3.1$, p = 0.08; Figure 2) and that the likelihood tended to increase the more they courted (Likelihood ratio, $\chi^2_1 = 3.2$, p = 0.08). Generally, across all trials, males that were attacked had courted nearly twice as much during a trial than males that were not attacked by *R. rabida* (attacked males: N = 31, $\bar{x} = 10.5 \pm 1.75$ bouts; non-attacked males: N = 18, $\bar{x} = 5.9 \pm 1.75$ bouts).

### *3.2. Experiment II: Predation risk and mating tactic expression*

Male *R. punctulata* mating tactic expression was dependent on their environmental treatment (overall Likelihood ratio model: $\chi^2_4 = 9.8$, p = 0.04).

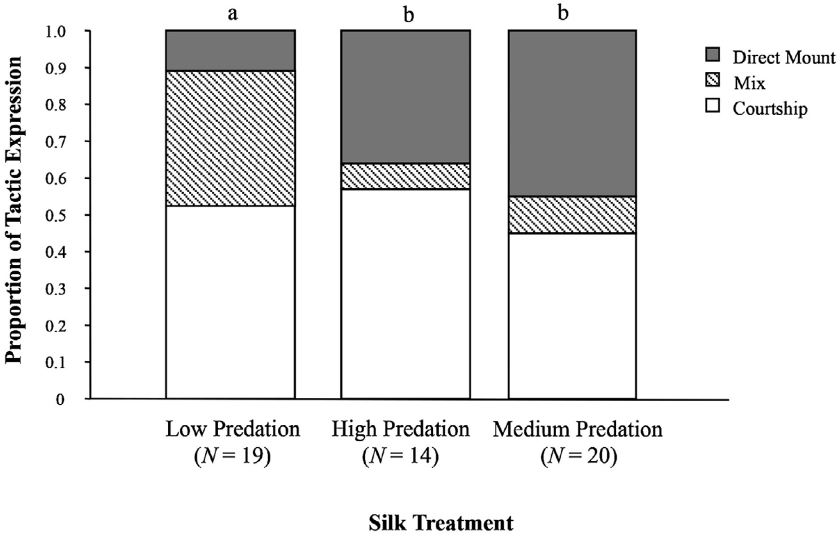

**Figure 3.** Influence of female silk type on frequencies of male mating tactics in *Rabidosa punctulata*. Silk cues were 100% conspecific female in the low predation treatment (LP), 100% predator silk in the high predation treatment (HP), and 50/50 conspecific/predator in the medium predation treatment (MP). Different letters denote significant differences ($p < 0.05$) as indicated by pairwise comparisons.

Male mating tactic frequencies expressed during trials in the low predation environment (LP) differed significantly compared to the frequencies expressed in the high predation environment (HP; Likelihood ratio, $\chi^2_2 = 5.9$, $p = 0.05$; Figure 3). When both silk types were detected together in the medium predation treatment (MP), we found that mating tactic frequencies were similar to that of HP (likelihood ratio, $\chi^2_2 = 0.5$, $p = 0.78$), but significantly differed from LP (Likelihood ratio, $\chi^2_2 = 7.8$, $p = 0.02$). In the presence of any predatory cues (HP or MP), males were 3–4-times more likely to employ the direct mount tactic when compared to males presented with conspecific silk (Figure 3). Overall, males were considerably more likely to court (combining courtship and mix tactics) when exposed to LP compared to the HP (Likelihood ratio, $\chi^2_1 = 5.2$, $p = 0.02$) or MP treatment (Likelihood ratio, $\chi^2_1 = 7.0$, $p = 0.008$; Figure 3). A secondary analysis confirmed that when predator silk was present (HP and MP), both mating tactics and likelihood to court was significantly different from when predator silk was absent (mating tactic: Likelihood ratio, $\chi^2_2 = 9.3$, $p = 0.01$; courtship: Likelihood ratio: $\chi^2_1 = 7.3$, $p = 0.007$).

For those males that courted, the latency to initiate courtship (LP: N = 17, $\bar{x}$ = 132.2 ± 93.2 s; HP: N = 9, $\bar{x}$ = 333.8 ± 128.1 s; MP: N = 11, $\bar{x}$ = 193.7 ± 105.4 s; Kruskal–Wallis test, $\chi^2_2 = 0.76$, $p = 0.69$) and the courtship rate (no. of courtship bouts/s; LP: N = 17, $\bar{x}$ = 0.023 ± 0.004 bouts/s; HP: N = 9, $\bar{x}$ = 0.016 ± 0.004 bouts/s; MP: N = 11, $\bar{x}$ = 0.015 ± 0.004 bouts/s; Kruskal–Wallis test, $\chi^2_2 = 2.87$, $p = 0.24$) were similar across all silk treatments.

Overall, males experienced similar probabilities of copulation regardless of what silk treatment they were on or what mating tactic they used (Overall Logistic Regression Model, $\chi^2_8 = 8.61$, $p = 0.38$).

## 4. Discussion

In this study, we found that a predator, female *R. rabida*, imposes a cost on courting male *R. punctulata*, and that this cost plays a role in mating tactic expression. Predatory heterospecific female *R. rabida* regularly attacked male *R. punctulata*, sometimes resulting in death; and courting in the presence of female *R. rabida* tended to increase a male's risk of being attacked. The detection of cues from these predatory heterospecifics also influenced the mating tactic expression of males. Male *R. punctulata* were more likely to adopt a direct mount mating tactic, forgoing courtship altogether, in the presence of silk cues from the predatory female *R. rabida*. This behavioral alteration did not reduce reproductive success, as copulation success was independent of mating tactic.

While actual predation occurrences during trials were low (approx. 6%), the regular and consistent attacks on male *R. punctulata* appear additionally costly due to injury (observed in this study) as well as increased energetic demands of long periods of grappling during attempted escapes. Nonetheless, even at low levels of occurrence, extreme costs (i.e., predation, cannibalism) from intraguild predators can have dramatic impacts on population dynamics (Wagner & Wise, 1996; Wise & Chen, 1999; Buddle et al., 2003; Persons & Uetz, 2005). We suggest that such a cost from heterospecific *R. rabida* may influence male courtship tactic deployment in *R. punctulata*. Past studies have shown that *R. rabida* use both visual and seismic cues in prey localization and capture (Lizotte & Rovner, 1988), making the visual and seismic courtship display of *R. punctulata* readily detectable and potentially quite conspicuous. Indeed, our results suggest that males who court in the presence of *R. rabida* tend to be more susceptible to attack; and that courting more often increased a male's risk. Courtship in *R.*

*punctulata* is not a quick tactic, even in the laboratory, as males often court for long periods of time in an effort to attract and convince a female to mate (Wilgers et al., 2009). The longer this activity persists, the more susceptible males are to attack from eavesdropping heterospecifics. Given this, one might predict that males would cease courtship, potentially switching to a direct amount, upon detecting cues from a predatory heterospecific. Such a potential sense of urgency, however, could lead to errors as males could mistakenly attempt to mount the approaching predator. Such a "mistake" was observed in our first experiment, resulting in the male being attacked. An interesting avenue for future studies would be a focus on male courtship adjustments with real-time exposure to heterospecific cues as well as an assessment of error rates (i.e., attempting to mount a heterospecific female) and their associated cost.

Observations of males using the direct mount tactic were low (compared to Wilgers et al., 2009), which likely reflects the increased complexity of the arenas for this experiment. Despite the reduction in direct mount observations in more natural habitat settings, this tactic has been documented in the wild (Fitch, 1963), and appears to represent a beneficial option for males as it allows them to reduce courtship activity in the presence of predatory heterospecifics so as to minimize associated mating costs while at the same time maintaining mating activity/success. This balance between the costs and benefits of a courtship tactic may explain why large, good condition males (who are extremely successful at acquiring a mate through courtship) would ever employ a direct mount tactic.

The observation that *R. punctulata* males alter their mating tactic in environments indicating heightened predation risk suggests that males can use silk cues as a means of assessing their environment. Mating tactic expression in the trials with predator silk present (MP, HP) differed from trials where it was absent (LP). Additionally, our data suggest that the difference in tactic expression is due to the spiders' ability to differentiate between silk types rather than simply due to the lack of conspecific silk. When multiple silk cues were detected (i.e., MP treatment), the presence of the predator, *R. rabida*, overrides the presence of conspecific *R. punctulata* as evidenced by the differences in tactic expression between the LP and MP treatments, while HP and MP were similar in the frequencies of tactics used. These results are similar to previous studies with wolf spiders where individuals were able to determine the identity of their audience (e.g., conspecific vs. heterospecific; Roberts & Uetz, 2004) and were able to assess potential risk through silk and excrement cues of heterospecifics (e.g., Persons et al., 2001; Bell et al., 2006). Silk pheromones are not airborne and volatile, which provides both direct localization of where the source used to be as well as an estimate of how long ago they were there (Tietjen, 1979b; Barnes et al., 2002). Future work investigating the sensitivity of male mating behaviors to temporal variation in silk deposition could provide better insight into this risk assessment and decision-making process.

The previously reported pattern of condition-dependent tactic expression in *R. punctulata* is atypical, where larger, good condition males use direct mounts rather than courtship, while smaller, poor condition males predominantly use courtship and do not generally engage in direct mounts likely due to increased risk of cannibalism (Wilgers et al., 2009). Given this, we highlight the fact that male trial masses were different across our treatments. However, the HP treatment had the lowest mean trial mass across treatments, which would lead to the highest predicted frequency of courtship based on the strong pattern of condition-dependent expression found previously (Wilgers et al., 2009). Instead, our findings directly contradict this, as we found the highest frequencies of direct mounts expressed in this treatment group. This suggests that the context of the mating encounter can be just as influential in determining a male's mating tactic expression as can his condition, especially if the associated costs are high enough.

In summary, we have shown that the condition-dependent mating tactics of male *R. punctulata* are also responsive to the mating context, at least in terms of perceived predation risk. We have shown that one mating tactic can incur significant costs through the eavesdropping of predatory heterospecifics and that males can adaptively adjust their tactic expression seemingly in response to this cost. In this way, the use of alternative mating tactics can enable males to avoid tactic-specific costs while not foregoing their reproductive effort altogether. Similar tactic-specific costs may be responsible for the evolution of alternative mating tactics in other groups as well.

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