2016. Journal of Arachnology 44:380–387

The effects of male competition on the expression and success of alternative mating tactics in the wolf spider *Rabidosa punctulata*

Sean De Young and **Dustin J. Wilgers**: Natural Sciences Department, McPherson College, 1600 E. Euclid, McPherson, KS 67460. E-mail: wilgersd@mcpherson.edu

Abstract. Alternative mating tactics are often expressed differentially based on a variety of factors associated with each mating context in order to maximize a male's reproductive success. In particular, males of many species attempt to reduce competition with males in the surrounding environment by altering their mating behaviors. In the wolf spider *Rabidosa punctulata* (Hentz, 1844), males exhibit two distinct mating tactics: 1) courtship—comprised of visual and seismic signals or 2) direct mount—involving males grappling with females for copulation. In natural environments, these spiders are relatively dense. Competing males are often close by and could potentially intercept courtship displays, locate the nearby female and steal the copulation. Here we investigate whether males adjust their mating tactic expression in response to indirect and directly competing males, and whether these decisions affect their likelihood to copulate. In both experiments, the actions of a competing male did not affect the expression of any male mating behaviors in the other, suggesting a lack of an effect of scramble competition on tactic expression. Evidence from our triad mating experiment suggests a mating advantage for males that adopt the direct mount tactic when in direct competition with other males. In particular, direct mounts were most successful when multiple males were actively pursuing a female and when adopted first among the competitors. Additionally, we observed direct male mating interference whereby the copulating pair was broken up. Following these breakups, females were observed to mate multiply, often as a result of a direct mount. This new observation may provide a context in which males benefit through additional copulations by adopting the direct mount tactic.

Keywords: Behavioral plasticity, social environment, intrasexual selection, multiple mating, male interference

Variation in factors intrinsic and extrinsic to the individuals involved has been found to affect female choice and mating probabilities (e.g., female/male age and condition, predators, environment, mate density; Jennions & Petrie 1997). This context-related variable reproductive success has favored the evolution of variable male mating behaviors (i.e., alternative mating tactics) that often vary considerably in form within a species (e.g., court vs. sneak, territorial vs. satellite). In many species, alternative mating tactic expression 1) depends on the context of the mating interaction, and 2) increases a male's reproductive success under these specific situations (reviews in Gross 1996; Brockman 2001). Specifically, tactic expression has been shown to be sensitive to variation in factors that are both intrinsic (e.g., condition, size, age) and extrinsic (e.g., predation, habitat, social environment) to individuals (e.g., Reynolds et al. 1993; Godin 1995; Rezucha & Reichard 2014; Sato et al. 2014; Brockmann et al. 2015). The context(s) that may have shaped the evolution and expression of mating tactics likely varies across species. Thus, in order to understand the conditions that may have favored the evolution of alternative mating tactics, it is important to understand the natural history of a species and the variety of context-specific reproductive benefits of each tactic.

One particularly influential context with regards to mating probabilities is the social environment. When attempting to find a mate, males often find themselves in competition with other males in their immediate vicinity. Male competition for fertilization of limited female eggs can occur at all points during the reproductive process, including pre-copulation scrambles for first access to mate with females, more direct agonistic behaviors and contests, mating interference of copulating pairs, and finally even post-copulation as the sperm collected by females from mating with multiple males compete to fertilize her eggs (Andersson 1994). This intense form of sexual selection has been an important driver of evolution of mating systems and a variety of traits related to reproduction (e.g., male size, ornamentation, weapons, sperm, behavior; Andersson 1994; Shuster & Wade 2003). How and whether this selection will manifest in mating behaviors will depend on when male competition is acting in each system, which will vary based on a species' natural history.

Pre-copulatory male competition for access to females often results in the evolution of variable mating behaviors due to the fitness benefits associated with this plasticity. Males commonly use broadcast courtship displays during courtship (Andersson 1994). The use of these broadcast displays, while known to attract the females they are directed toward, tend to also attract eavesdropping males, thus increasing competition (i.e., social facilitation; Balsby & Dabelsteen 2005; Milner et al. 2010; Clark et al. 2012). Selection should favor any alteration in male behaviors that reduces competition and thus enhances the likelihood of mating. We know that in many cases, males across the animal kingdom alter mating behaviors in response to the social environment in efforts to reduce competition with surrounding males. The presence of competing males is known to alter male courtship activity (reduce: e.g., Cade & Cade 1992; Barnett & Pankhurst 1996; Wong 2004; increase: e.g., Ridgeway & McPhail 1987; Sadowski et al. 2002; Desjardins et al. 2012), match their rival's displays (e.g., Clark et al. 2012), change display location (Dzieweczynski & Rowland 2004), or move to less competitive social networks (Bel-Venner et al. 2008; Oh & Badyaev 2010; Jordan et al. 2014). Across several taxa, males often adopt alternative mating tactics (e.g., sneaker, satellite, female mimic) that circumvent competition with rivals for access to females (e.g., Christenson & Goist 1979; Wagner 1992; Emlen 1997; Evans & Magurran 1999;

Correa et al. 2003; Auld et al. 2015). For example, in the redback spider, *Latrodectus hasselti* Thorell, 1870, when in the presence of rival males, inferior males forgo courtship and aggressive interactions to attempt sneak copulations with females (Stoltz et al. 2008; 2009). While these alternative tactics often achieve lower levels of reproductive success compared to other males (e.g., Christenson & Goist 1979; Whitehouse 1991; Brockman et al. 1994; but see Rowell & Cade 1993; Gress et al. 2014), this behavioral alteration increases individual fitness given the mating context (e.g., male condition, social environment) when compared to other alternatives (i.e., best of a bad job; Dawkins 1980; Gross 1996; examples: Berard et al. 1994; Oh & Badyaev 2010; Jordan et al. 2014). These alternative tactics are a successful strategy as they reduce costs associated with intrasexual competition while gaining copulations with females. The reproductive benefits associated with these behavioral alterations in response to the social environment could have been an important driver in the evolution of alternative mating tactics in many systems (Shuster & Wade 2003; Taborsky et al. 2008).

The mating systems of many wolf spider species are characterized as polygynous scramble competition (Roberts & Uetz 2005), whereby males are competing to locate and mate with relatively monandrous females first (Norton & Uetz 2005). In the wolf spider, *Rabidosa punctulata* (Hentz, 1844) (Araneae: Lycosidae), populations are often quite dense in their grassland habitats, with multiple males often seen in close proximity to a female, suggesting the potential for strong pre-mating scramble competition (Wilgers, pers. obs.). Upon detection of female silk (i.e., a female is/has been in the area), male *R. punctulata* often use a multimodal courtship display, which could increase mate competition if nearby males are eavesdropping. However, male *R. punctulata* are known to adopt alternative mating tactics, forgoing courtship by directly grabbing females and often grappling with them for copulation (Nicholas 2007). Direct mounts achieve copulation faster than courtship without broadcasting the presence of a female first (Wilgers et al. 2009), which could benefit males if competitors are nearby. The expression of these mating tactics has been found to be dependent on other variables, as their expression is sensitive to the male's condition (Wilgers et al. 2009) and the proximity of a predator (Wilgers et al. 2014). In each case, a male expresses the tactic that increases his chance at copulation while limiting the costs associated with that scenario, reducing the risk of cannibalism or potential detection by nearby predators. The potential tactic-specific costs and benefits associated with male-male competition suggest that mating tactic expression should be responsive to the social context of mating encounters as well. Use of the direct mount tactic should increase a male's reproductive success when faced with competing males in the environment by increasing his chance to copulate. Thus, upon detection of rivals, males would be predicted to adopt a direct mount tactic more frequently than courtship.

Here we test these hypotheses by investigating how 1) the social environment influences the mating tactics used during mating interactions, and 2) these mating tactic decisions affect a male's chances to copulate. The results from this study may shed light on how different types of male competition may have played a role in the evolution of alternative mating tactics in *R. punctulata*.

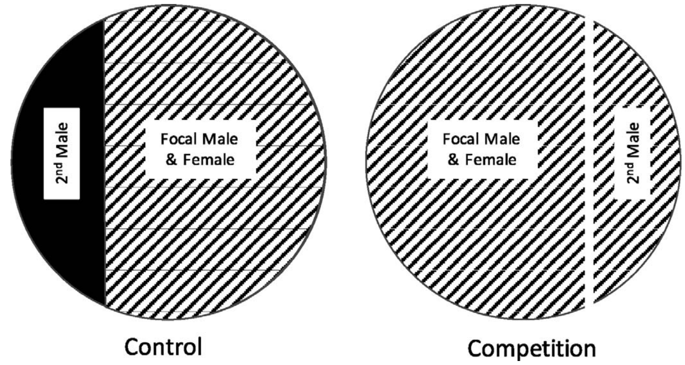

Figure 1.—Trial arenas used to investigate the effects of the presence of competing males on mating tactic expression in *Rabidosa punctulata*. Regions of arena with diagonal pattern indicate areas of floor covered with female-silk laden filter paper. Black regions of the arena indicate a granite arena floor. The barrier between the focal and secondary male compartments did not allow visual contact in either treatment. Arena dimensions: diameter = 20.2 cm, height = 7.3 cm.

METHODS

Spider collection and maintenance.—We collected over 300 immature *R. punctulata* on 23–24 August 2013 from Lancaster County, Nebraska. Upon collection, the spiders were taken to the lab and individually housed in plastic containers (8.4 × 8.4 × 11.0 cm) and were visually isolated from other conspecifics. Spiders were provided with water *ad libitum* and were fed 2–3 body-size matched crickets per week. All crickets were supplemented with Flukers® cricket feed (Port Allen, LA). We placed all spiders in a climate-controlled room (21–24° C) under a 14:10 light-dark cycle. Spiders were checked every 2–3 days for molts until maturation.

Experiment 1: Detection of competing male.—In order to examine how scramble competition may affect mating tactic expression, we tested whether the detection of a courting male alters a male's mating tactic expression when interacting with a female. To do this, we exposed males to one of two treatments: 1) Competition, where a courting male could be detected in the arena, or 2) Control, where no other male was detected. All trials were conducted in circular plastic arenas (Fig. 1; diameter = 20.2 cm, height = 7.3 cm; Pioneer Plastics) with granite floors. Trial arenas were split into two compartments, one for the interacting focal male and female, and the second for a secondary male. The structure of both the competition and control arenas were identical with the exception of the presence of filter paper connecting the focal male and secondary male compartments (Fig. 1). In the control treatment, there was no filter paper on the floor of the secondary male compartment; while in the competition treatment, filter paper (Whatman #1, 185 mm) with female silk cues (see below) lined the entire arena floor. Female silk is known to elicit male courtship displays even in the absence of females (Tietjen 1977). This setup induced the secondary male to court, allowing the focal males in the competition group to detect courting secondary males via seismic cues, but not visual cues, thanks to a connected substrate and opaque arena walls. Males in the control group could not detect a second male present because the granite substrate effectively ablates the seismic cues caused by male movement, including courtship (Elias et al. 2004; Wilgers & Hebets 2011). Trials were always performed in pairs, consisting of a competition and control trial run simultaneously.

Prior to trials, we weighed all spiders to the nearest .001 g on an electronic scale (Denver Instruments Company, TR-603D). Females were then placed in a container to allow them to acclimate and deposit pheromone-laden silk onto filter paper for at least one hour before the experiment began. After this time period, the filter paper (of appropriate treatment size) was laid in the trial arena and the secondary males were introduced to their arena compartment. Once the competition secondary male began courting, the focal male and female for both treatments were placed into their respective arenas and the trial began.

Trials lasted 30 minutes, or until copulation occurred. If copulation occurred, that individual trial was done, but the other of the pair continued until 30 minutes or copulation occurred. The following behaviors were recorded for every trial: tactic used by the focal male (courtship, direct mount, or mixed tactic where both were used in a trial), latency (s) to each tactic, number of courtship bouts of the focal male, number of courtship bouts of the secondary male (competition treatment only), number of attacks by the female, copulation (yes, no), and latency (s) to copulation. All individuals used in each trial were virgins and had not come into contact with a mature individual of the opposite sex. All individuals were only used once. After each trial, the filter paper was disposed of and the arenas were cleaned with ethanol to remove silk cues and excreta.

Data analysis: We used likelihood ratio tests to analyze the effects of our treatments (competition vs. control) on several categorical response variables, including the overall mating tactic (courtship, direct mount, mixed), the first tactic used (courtship, direct mount), copulation success (yes, no), and the tactic used to gain copulation (courtship, direct mount). We used non-parametric tests to compare the control and experimental groups for the following continuous variables: female age & weight, focal male age & weight, courtship latency, number of courts, and copulation latency. Statistical tests were performed in JMP (version 6.0, SAS Institute). All results are reported as mean ± standard error.

Experiment 2: Direct male competition.—In order to examine how both scramble and direct competition with other males may affect male mating behaviors, tactic expression and mating success, we used a triad mating experiment and observed the mating success of each male based on his expressed tactic. The triad (i.e., 2-choice) mating experiment allowed two males and one female to directly interact. This experimental design has been used in other spider studies that explore mating success based on a variety of male attributes (e.g., size, ornamentation; Hebets et al. 2008; Shamble et al. 2009). Unlike other studies, we did not manipulate male characters or intentionally set up dichotomous males; instead we allowed males to naturally express a mating tactic based on the context and we then observed their success in acquiring the copulation with the sole female. Male ages ranged from 29–54 days post maturation ($\bar{x} = 36.4$ days), and only differed in age in four pairings ($\bar{x} = 0.56$ days). Males were generally the same size, on average only being 0.027 g different, and these differences did not influence mating success (Likelihood ratio, $\chi^2_1 = 0.4$, $P = 0.85$).

All trials were conducted in a circular plastic arena (diameter = 20.2 cm, height = 7.3 cm; Pioneer Plastics) with a floor lined with filter paper (Whatman #1, 185 mm). Prior to trials, all individuals were weighed to the nearest 0.001g on an electronic scale (Denver Instruments Company, TR-603D). Both males were marked with a dot on the dorsal surface of the cephalothorax with either a yellow or white painter's pen (Elmer's® Painters marker) to facilitate individual identification and tracking throughout the trial. Males were gently restrained in a resealable food storage bag and marked through a hole in the bag. Females were introduced to the arena one hour prior to the trial in order to acclimate and deposit pheromone-laden silk. Males were introduced to the trial arena in separate opaque glass vials. After one minute for acclimation, both vials were removed simultaneously and the trial began.

Trials lasted 30 minutes unless copulation occurred. We found interesting interactions after copulation during the first 7 trials, so for the final 20 trials we extended these trials for 10 minutes beyond a copulation to allow the second male to interact with the copulating pair (19/20 copulated). The following behaviors were recorded for every trial: tactic used by each male, latency (s) to each tactic, number of courtship bouts by each male, number of attempted mounts by each male, number of attacks by the female on each male, copulation (yes/no), and latency (s) to copulation. After a copulation occurred, we recorded the number of break up attempts by the second male, if and when the copulation was successfully broken up, and if broken up, whether a second copulation occurred, which male acquired this copulation, and the tactic used to gain the second copulation. All individuals used in each trial were naïve virgins. All individuals were used in trials only once. After each trial, the filter paper was disposed of and the arenas and glass vials were cleaned with ethanol to remove silk cues and excreta.

Data analysis: Because we were examining how differences in behaviors of competing males resulted in copulation success, we only included in our analyses trials that resulted in copulation. We used separate likelihood ratio tests to analyze the effects of expressed tactic and competing male behaviors on male copulation success. All other tests were nonparametric. Statistical tests were performed in SPSS (version 21, IBM®). All results are reported as mean ± standard error.

RESULTS

Experiment 1: Detection of competing male.—In total, 36 trials were conducted ($N = 18$/treatment). The focal males used in our experiment were similar across both of the treatment groups in age (Control: $\bar{x} = 36.3 \pm 1.5$ days; Competition: $\bar{x} = 36.0 \pm 1.7$ days; Wilcoxon 2-sample test, $Z = 0.64$, $P = 0.52$) and weight (Control: $\bar{x} = 0.127 \pm 0.007$ g; Competition: $\bar{x} = 0.119 \pm 0.005$ g; Wilcoxon 2-sample test, $Z = 0.32$, $P = 0.75$). Likewise, the secondary males used in each treatment were similar in both age (Control: $\bar{x} = 38.9 \pm 2.8$ days; Competition: $\bar{x} = 37.1 \pm 1.6$ days; Wilcoxon 2-sample test, $Z = 0.24$, $P =$

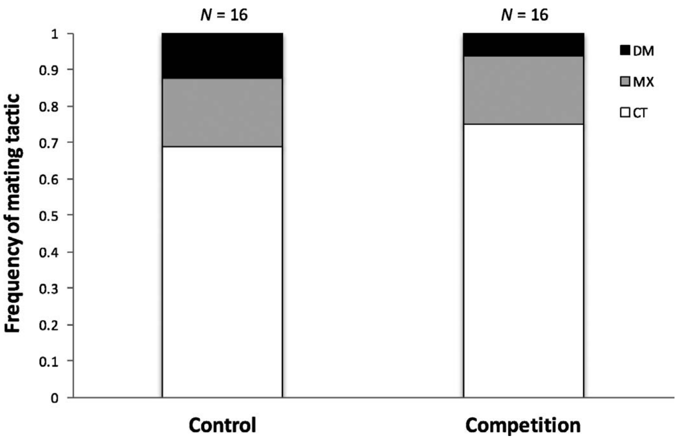

Figure 2.—The effects of competing males on mating tactic expression by male *R. punctulata*. There was no significant difference in the mating tactics expressed between the control and competition treatments (P = 0.83). CT= Courtship, DM= Direct Mount, MX= Mixed Tactic.

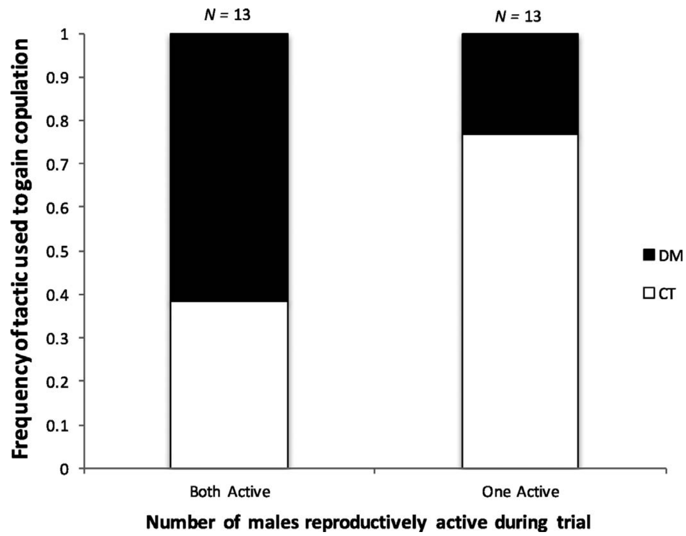

Figure 3.—Mating success of male mating tactics during triad mating trials based on the number of males that were reproductively active. The most successful mating tactic during trials was dependent on the number of males active during the trial (P = 0.04). CT= Courtship, DM= Direct Mount.

0.815) and weight (Control: $\bar{x} = 0.115 \pm 0.005$ g; Competition: $\bar{x} = 0.133 \pm 0.008$ g; Wilcoxon 2-sample test, $Z = 1.72$, $P = 0.09$). The females were also similar across both of the treatment groups in age (Control: $\bar{x} = 33.11 \pm 1.54$ days; Competition: $\bar{x} = 32.83 \pm 1.63$ days; Wilcoxon 2-sample test, $Z = 0.19$, $P = 0.85$) but not weight as control females were heavier (Control: $\bar{x} = 0.223 \pm 0.0071$ g; Exposed: $\bar{x} = 0.200 \pm 0.0079$ g; Wilcoxon 2-sample test, $Z = 2.03$, $P = 0.04$).

Exposure to a courting male in the environment did not affect the mating tactic expression of focal males; the frequencies of mating tactics witnessed were similar across our two treatments (Fig. 2; Likelihood ratio, $\chi^2_2 = 0.38$, $P = 0.83$). In four trials, males did not express a mating tactic during the trial. Exposure to a courting male did not affect this non-activity, as they were equally distributed between both treatments (N = 2 for control and experimental groups). Similarly, exposing a courting male in the environment did not affect which mating tactic was used first by the focal males; the frequencies of mating tactics witnessed were similar across both treatments (Likelihood ratio, $\chi^2_1 = 0$, $P = 1.0$). Variation in secondary male courtship effort did not affect the mating tactic expression of the focal males in the competition group, as no relationship was detected (Logistic regression; $\chi^2_3 = 2.10$, $P = 0.55$). In addition, both the focal male's latency to courtship (Control: $\bar{x} = 306 \pm 72.22$; Competition: $\bar{x} = 519 \pm 124.6$; Wilcoxon 2-sample test, $Z = 1.00$, $P = 0.32$) and the focal male's number of courtship bouts were similar across both treatments (Control: $\bar{x} = 21.64 \pm 3.97$; Competition: $\bar{x} = 23.53 \pm 15.11$; Wilcoxon 2-sample test, $Z = 0.24$, $P = 0.81$).

The presence of an additional courting male did not affect the likelihood or latency of copulation by the focal male. Both mating frequencies (Control: 61%; Competition: 50%; Likelihood ratio, $\chi^2_1 = 0.45$, $P = 0.50$) and latency to copulate were similar across both treatments (Control: $N = 11$, $\bar{x} = 797 \pm 167$; Competition: $N = 9$, $\bar{x} = 980 \pm 149$; Wilcoxon 2-sample test, $Z = 0.99$, $P = 0.32$). The mating tactics used by the focal males to successfully gain copulations were also similar across both treatments (Control: courtship = 82%, direct mount = 18%; Competition: courtship = 78%, direct mount = 22%; Likelihood ratio, $\chi^2_1 = 0.05$, $P = 0.82$).

Experiment 2: Direct male competition.—In total, 27 trials were conducted, of which 96% resulted in copulation. Males directly interacted with each other during 62% of trials. Male attacks on the other male were common (30% of trials), but not as common as males attempting to mount the other male (42% of trials).

Males expressed some reproductive behaviors in all trials. The frequencies of tactics that were expressed first were not equal ($\chi^2_1 = 15.39$, $P < 0.001$). The most common first tactic used during a trial was courtship (N = 23/26). The tactic expressed by the first male did not significantly influence the behavior of the second male (Likelihood ratio, $\chi^2_2 = 4.55$, $P = 0.10$). However, the frequency of male's not adopting a mating tactic tended to be higher following a direct mount (2nd male tactic, $N = 3$: None 100%, Courtship = 0%, Direct Mount = 0%) when compared to after courtship (2nd male tactic, $N = 23$: None = 43.4%, Courtship = 39.1%, Direct Mount = 17.4%). Both males expressed a mating tactic during the trial in 50% of trials (N =13). The most successful tactic at gaining the copulation during a trial depended on how many males were reproductively active (Likelihood ratio, $\chi^2_1 = 4.06$, $P = 0.04$). When only one male was active, courtship was the most successful tactic, as it gained copulations more often; however, when both males were active, the direct mount tactic was more commonly used to acquire the copulation (Fig. 3).

Being the first male to express a tactic affected copulation success in different ways depending on the tactic being expressed. Males that were the first to adopt the direct mount tactic were significantly more likely than their competitor to gain the copulation in the trial (Fig. 4a; $\chi^2_1 = 5.56$, $P = 0.02$). However, males that were the first to adopt courtship were no more likely than their competitor to gain the copulation in the trial (Fig. 4b; Likelihood ratio, $\chi^2_1 = 1.53$, $P = 0.22$). Likewise, differential courtship intensity did not affect mating success,

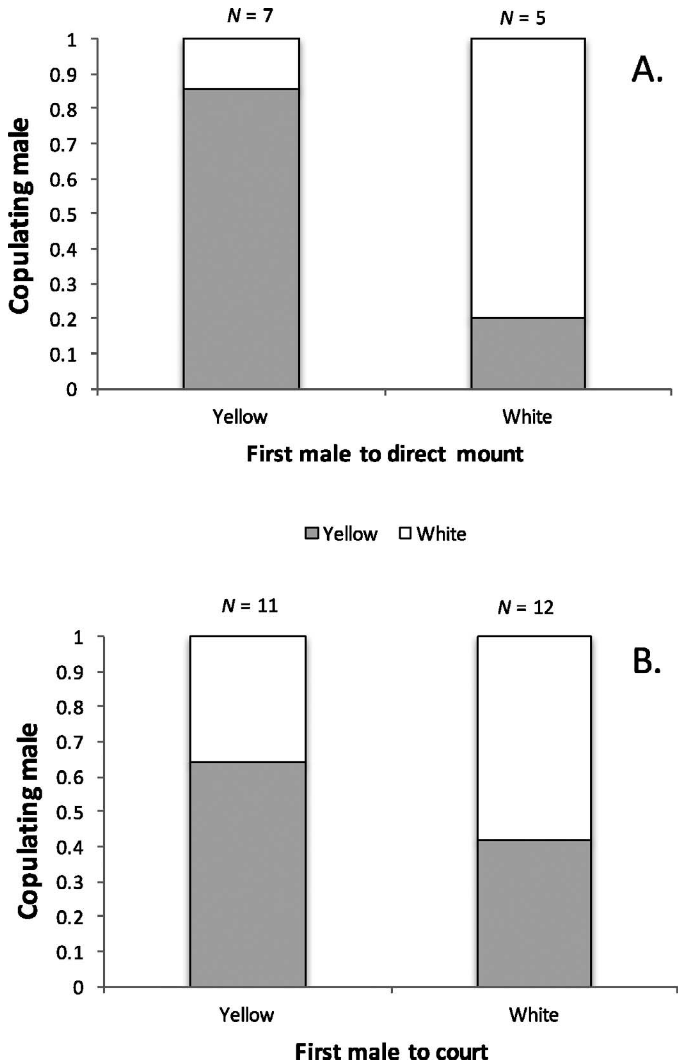

Figure 4.—Mating success of male mating tactics during triad mating trials based on the first male to adopt (A) the direct mount tactic or (B) courtship. The x-axis groups are based on the identification color randomly assigned to each male (yellow or white). The color inside the bars represents the proportion of males in each color that copulated under each circumstance. If order of action affects mating success, one would expect the color of the copulating male to match the color of the first male to act. This occurred in the direct mount tactic ($P = 0.02$), but not in the courtship tactic ($P = 0.22$).

as males that courted more intensely were no more likely to copulate than the other male in the trial (Court More-Copulate Match: 4/7, Court More-Copulate No Match: 3/7; Goodness of Fit, $\chi^2_1 = 0.14$, $P = 0.71$).

Of the 19 trials we observed following copulation, the second male attempted to directly break up the trial in 63% of them, often attempting to break up the pair multiple times ($\bar{x} = 1.89$ / trial overall). Males that attempted to break up the pair were successful in 50% of trials (6/12), with one of those break ups occurring before the initial copulating male inserted a pedipalp for sperm transfer (18 s post 1st male mount). After the pair was broken up, females were remounted for a 2nd copulation 83% (5/6 trials) of the time, with three of those 2nd copulations occurring with the other male in the trial. The tactic used for the first copulation was similar across the females that accepted a second copulation ($N = 3$ courtship, $N = 2$ direct mount). The direct mount tactic was the most successful tactic at gaining the 2nd copulation (80% of attempts; 4/5 trials). The only time a female accepted a courting male for a 2nd mounting was after the mating attempt that was broken up prior to pedipalp insertion.

DISCUSSION

In this study, we found differing effects of indirect and direct male competition on tactic-specific copulation success in *R. punctulata*. Despite this tactic-specific success, males did not alter their mating tactic expression in response to competing males in the environment. We found evidence that when males avoided courtship and took a more direct mating tactic, they had a mating advantage when directly competing with males in the environment, but not when courting males were simply nearby. Using the direct mount tactic increased the likelihood of gaining copulations over the courtship tactic when 1) multiple males in the surrounding environment had expressed some mating behaviors, and 2) when the male was the first one to attempt it. Additionally, we witnessed direct male interference during our trials. In some trials, competing males not only broke up copulating pairs, but would then gain copulations with females, most often by using a direct mount.

When multiple *R. punctulata* males are in close proximity and directly competing for a female, it is clear that engaging the female and using a direct mount tactic offers mating advantages. When directly competing with another male, no aspect of the courtship tactic that we measured increased a male's chance at copulation when competing with other males either indirectly or directly. In other wolf spider species, both the latency to begin courtship (negative relationship) and courtship intensity (positive relationship) have been linked with copulation success (e.g., Scheffer et al. 1996: Shamble et al. 2009). The direct mount tactic appears to be successful at achieving copulations by eliminating one variable that males cannot control, female approach. In *R. punctulata* and another closely related species, *R. rabida* (Walckenaer, 1837), females will approach courting males and often settle receptively (Rovner 1968; Wilgers pers. obs.). By approaching and grabbing females upon detection, males can ensure other males in the surrounding environment will not find her first. This conclusion is supported by the observations that courtship is only successful when one male is reproductively active, allowing more time for the courtship process. Instead, when both males were active, direct mounts were more successful and the male to adopt the direct mount tactic first more often gained the copulation.

The mating advantage associated with direct mounts when in competition with other males does not appear to be a strong enough source of selection to have affected tactic-expression patterns. Across both experiments, we found no evidence of pre-mating male-male competition. Males that were both directly and indirectly competing with males in their environment did not adjust their pre-mating behaviors. This absence of a response to competing males has also been seen in the wolf spider *Schizocosa ocreata* (Hentz, 1844) (Roberts et al. 2006). We also found no evidence of consistent agonistic behaviors between males. Instead, we found that males mistakenly mounted the competing male as often as they attacked them. In other spider species, males often engage competing males directly with agonistic behaviors (Aspey 1977a, b; Christenson & Goist 1979; Rovner 1996; Uetz et al. 1996); however, evidence that outcomes of these aggressive encounters result in copulation is lacking (Kotiaho et al. 1997; Delaney et al. 2007).

Instead, in *R. punctulata* it appears that male competition comes in the form of male interference during copulations and sperm competition from multiple mating. Interference competition is prevalent in the animal kingdom and males of other spider species have been witnessed to disrupt copulating pairs (e.g., Lubin 1986; Foellmer & Fairbairn 2005). When detected, male *R. punctulata* clearly disrupted the copulating pair and then attempted to mate with the female afterwards. While 80% of second matings during the trial came from direct mounts, due to a limited sample size we were unable to statistically test the differential success of the mating tactics following mating interference. Future studies should more explicitly test the benefits of direct mounts following mating interference. While copulation interference is a striking behavior, it is not clear how common it is in nature, as copulating pairs are not nearly as obvious in their natural environment. In order to estimate its importance in sexual selection, it will be necessary to estimate rates of mating interference in the field.

Our limited results suggest that it may be beneficial for males to adjust their tactic and increase the use of direct mounts following mating pair breakups or already mated females. The only trial in which a female receptively approached a courting male was after a copulation attempt was broken up prior to sperm transfer. Interestingly, females of a closely related species, *R. rabida*, are not only unreceptive to courting males as well, but often very aggressive after mating once (D. Wilgers, unpub. data). Males that are able to assess the mating status of females could benefit from adjusting their mating tactic accordingly by direct mounting already mated and potentially unreceptive females. In the wolf spider *Schizocosa ocreata*, the limited rematings observed often came from more coercive male behaviors (Norton & Uetz 2005). Males of other spider species have been shown to be able to assess female mating status through chemical cues in her silk (e.g., Roberts & Uetz 2005; Stoltz et al. 2007). Future research should investigate if male *R. punctulata* are sensitive to this information during their mating interactions and if they adjust their mating tactic expression accordingly to maximize fitness.

In our study, if given the opportunity to copulate again shortly after mating the first time, females often ($> 80\%$) copulated again. The observation that females will mate multiply is new to the species. Future studies should investigate female mating rates with longer periods of time between mating interactions. When females mate multiply, the scramble competition between males for the only copulation with a female is relaxed, but multiple mating by females introduces another form of male competition, post-copulatory sperm competition, where sperm from multiple males compete to fertilize a limited number of female eggs (Shuster & Wade 2003; examples in spiders: Schneider et al. 2000; Snow et al. 2006). In female spiders, male sperm is stored in the spermethecae, and in some species, females often store sperm from each mating separately, leaving the ability to control sperm release from these independent compartments (Eberhard 2004; Snow & Andrade 2005; Useta et al. 2007). By controlling sperm use post-mating, this more cryptic form of female choice could have dramatic consequences for the fitness of each male she has mated with (Eberhard 1996; examples in spiders: Welke & Schneider 2009; Peretti & Eberhard 2010). Male mating behaviors prior to copulation are known to affect female storage and use of their sperm (Watson 1991). In fact, in other taxa, the use of coercive tactics by males often leads to low fertilization success (e.g., fowl: Pizarri & Birkhead 2000; guppies: Evans & Magurran 2001). However, given the interesting condition-dependent expression and intimate nature of the direct mount tactic (i.e., good-condition males tend to direct mount; Wilgers et al. 2009), female *R. punctulata* could use the direct mounts as a form of assessment in determining the father of her offspring and we may expect a reversal in this sperm use pattern. First male sperm precedence is suggested in wolf spiders (Austad 1984; Rypstra et al. 2003); however, the determinants (e.g., mating order, male qualities) of sperm precedence in this species, which have yet to be determined, may result in reduced benefits of being the first mate (Eberhard 1996). Thus, the benefits of gaining that first mating may no longer outweigh the potential costs of grappling with a cannibalistic female for some males. While this paper only followed copulation success due to tactic-expression, which limits our discussion of tactic-related fitness consequences, it is clear that this mating system has many more questions to answer after the observations suggest more promiscuity than once thought. Investigations into the determinants of cryptic female choice (sperm precedence, male mating behavior, size, etc.) may provide considerable insight into the evolution of these mating behaviors. It is possible the optimal tactic may not depend on the social context, and may instead reflect some other factor associated with the mating interaction (e.g., male condition, female mating status), potentially explaining the lack of males adjusting their mating tactic to a more successful one based on the presence of direct competitors.

ACKNOWLEDGMENTS

Thanks to the Natural Sciences Department of McPherson College for funding this project. Thanks to Jonathan Frye, Allan Ayella, Allan van Asselt, Manjula Koralegedara, Kasey Fowler-Finn, Steven Schwartz and two anonymous reviewers for comments on earlier versions of this manuscript. Thanks to Eileen Hebets for allowing us to collect spiders on her property and to Christian Rodriguez for help in collecting the spiders.

LITERATURE CITED

Andersson, M. 1994. Sexual Selection. Princeton University Press. Princeton.

Aspey, W.P. 1977a. Wolf spider sociobiology. I. Agonistic display and dominance-subordinance relations in adult male *Schizocosa crassipes*. Behaviour 62:103–141.

Aspey, W.P. 1977b. Wolf spider sociobiology. II. Density parameters influencing agonistic behavior in *Schizocosa crassipes*. Behaviour 62:143–162.

Auld, H.L., S.B. Jeswiet & J.G.J. Godin. 2015. Do male Trinidadian guppies adjust their mating tactics in the presence of a rival male audience? Behavioral Ecology and Sociobiology 69:1191–1199.

Austad, S.N. 1984. Evolution of sperm priority patterns in spiders. Pp. 223–249. *In* Sperm Competition and the Evolution of Animal Mating Systems. (R.L. Smith, ed.). Academic Press, New York.

Balsby, T.J.S. & T. Dabelsteen. 2005. Simulated courtship interactions elicit neighbor intrusions in the whitethroat, *Sylvia communis*. Animal Behaviour 69:161–168.

Barnett, C.W. & N.V. Pankhurst. 1996. Effect of density on the reproductive behaviour of the territorial demoiselle *Chromis dispulis* (Pisces: Pomacentridae). Environmental Biology of Fishes 46:343–349.

Bel-Venner, M.C., S. Dray, D. Allaine, F. Menu & S. Venner. 2008. Unexpected male choosiness for mates in a spider. Proceedings of the Royal Society B 275:77–82.

Berard, J.D., P. Nurnberg, J.T. Epplen & J. Schmidtke. 1994. Alternative reproductive tactics and reproductive success in male rhesus macaques. Behaviour 129:177–201.

Brockman, H.J. 2001. The evolution of alternative strategies and tactics. Advances in the Study of Behavior 30:1–51.

Brockman, H.J., T. Colson & W. Potts. 1994. Sperm competition in horseshoe crabs (*Limulus polyphemus*). Behavioral Ecology and Sociobiology 35:153–160.

Brockmann, H.J., S.L. Johnson, M.D. Smith & D. Sasson. 2015. Mating tactics of the American horseshoe crab. Pp. 321–351. *In* Changing Global Perspectives on Horseshoe Crab Biology, Conservation, and Management. (R. H. Carmichael, M. L. Botton, P. K. S. Shin, S. G. Cheung, eds.). Springer International Publishing, Heidelberg.

Cade, W.H. & E.S. Cade. 1992. Male mating success, calling and searching behaviour at high and low densities in the field cricket, *Gryllus integer*. Animal Behaviour 43:49–56.

Christenson, T.E. & K.C. Goist Jr. 1979. Costs and benefits of male-male competition in the orb-weaving spider, *Nephila clavipes*. Behavioral Ecology and Sociobiology 5:87–92.

Clark, D.L, J. A. Roberts & G.W. Uetz. 2012. Eavesdropping and signal matching in visual courtship displays of spiders. Biology Letters 8:375–378.

Correa, C., J.A. Baeza, I.A. Hinojosa & M. Thiel. 2003. Male dominance hierarchy and mating tactics in the rock shrimp *Rhynchocinetes typus* (Decapoda: Caridea). Journal of Crustacean Biology 23:33–45.

Dawkins, R. 1980. Good strategy or evolutionary stable strategy. Pp. 331–367. *In* Sociobiology: Beyond Nature/Nurture. (G. W. Barlow, J. Silverberg, eds.). Westview Press, Boulder, Colorado.

Delaney, K.J., J.A. Roberts & G.W. Uetz. 2007. Male signaling behavior and sexual selection in a wolf spider (Araneae: Lycosidae): a test for dual functions. Behavioral Ecology and Sociobiology 62:67–75.

Desjardins, J.K., H.A. Hofmann & R.D. Fernald. 2012. Social context influences aggressive and courtship behavior in a cichlid fish. PLoS One 7:e32781.

Dzieweczynski, T.L. & W.J. Rowland. 2004. Behind closed doors: use of visual cover by courting male three-spined stickleback, *Gasterosteus aculeatus*. Animal Behaviour 68:465–471.

Eberhard, W.G. 1996. Female Control: Sexual Selection by Cryptic Female Choice. Princeton University Press. Princeton.

Eberhard, W.G. 2004. Why study spider sex: special traits of spiders facilitate studies of sperm competition and cryptic female choice. Journal of Arachnology 32:545–556.

Elias, D.O., A.C. Mason & R.R. Hoy. 2004. The effect of substrate on the efficacy of seismic courtship signal transmission in the jumping spider *Habronattus dossenus* (Araneae: Salticidae). Journal of Experimental Biology 207:4105–4110.

Emlen, D.J. 1997. Alternative reproductive tactics and male-dimorphism in the horned beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). Behavioral Ecology and Sociobiology 41:335–341.

Evans, J.P. & A.E. Magurran. 1999. Male mating behaviour and sperm production characteristics under varying sperm competition risk in guppies. Animal Behaviour 58:1001–1006.

Evans, J.P. & A.E. Magurran. 2001. Patterns of sperm precedence and predictors of paternity in the Trinidadian guppy. Proceedings of the Royal Society B 268:719–724.

Foellmer, M.W. & D.J. Fairbairn. 2005. Competing dwarf males: sexual selection in an orb-weaving spider. Journal of Evolutionary Biology 18:629–641.

Godin, J.G.J. 1995. Predation risk and alternative mating tactics in male Trinidadian guppies (*Poecilia reticulata*). Oecologia 103:224–229.

Gress, B.E., R.J. Waltzer, S. Lupold, E.M. Droge-Young, M.K. Manier & S. Pitnick. 2014. Alternative mating tactics in the yellow dung fly: resolving mechanisms of small male advantage off pasture. Proceedings of the Royal Society B 281: 20132164

Gross, M.R. 1996. Alternative reproductive strategies and tactics: diversity within sexes. Trends in Ecology and Evolution 11:92–98.

Hebets, E.A., J. Wesson & P.S. Shamble. 2008. Diet influences mate choice selectivity in adult female wolf spiders. Animal Behaviour 76:355–363.

Jennions, M.D. & M. Petrie. 1997. Variation in mate choice and mating preferences: a review of causes and consequences. Biological Review 72:283–327.

Jordan, L.A., H. Kokko & M. Kasumovic. 2014. Reproductive foragers: male spiders choose mates by selecting among competitive environments. American Naturalist 183:638–649.

Kotiaho, J., R.V. Alatalo, J. Mappes & S. Parri. 1997. Fighting success in relation to body mass and drumming activity in the male wolf spider *Hygrolycosa rubrofasciata*. Canadian Journal of Zoology 75:1532–1535.

Lubin, Y.D. 1986. Courtship and alternative mating tactics in a social spider. Journal of Arachnology 14:239–257.

Milner, R.N.C., M.I.D. Jennions & P.R.Y. Backwell. 2010. Eavesdropping in crabs: an agency for lady detection. Biology Letters 6:755–757.

Nicholas, A.C. 2007. The evolution of maternal investment among Lycosid spiders and mating behaviors in *Rabidosa punctulata*. Dissertation. University of Mississippi, Oxford.

Norton, S. & G.W. Uetz. 2005. Mating frequency in *Schizocosa ocreata* (Hentz) wolf spiders: evidence for a mating system with female monandry and male polygyny. Journal of Arachnology 33:16–24.

Oh, K.P. & A.V. Badyaev. 2010. Structure of social networks in a passerine bird: consequences for sexual selection and the evolution of mating strategies. The American Naturalist 176:E80–E89.

Peretti, A.V. & W.G. Eberhard. 2010. Cryptic female choice via sperm dumping favours male copulatory courtship in a spider. Journal of Evolutionary Biology 23:271–281.

Pizarri, T. & T.R. Birkhead. 2000. Female feral fowl eject sperm of subdominant males. Nature 405:787–789.

Reynolds, J.D., M.D. Gross & M.J. Coombs. 1993. Environmental conditions and male morphology determine alternative mating behaviour in Trinidadian guppies. Animal Behaviour 45:145–152.

Rezucha, R. & M. Reichard. 2014. The effect of social environment on alternative mating tactics in male Endler's guppy, *Poecilia wingei*. Animal Behaviour 88:195–202.

Ridgeway, M.S. & J.D. McPhail. 1987. Rival male effects on courtship behavior in the Enos Lake species pair of sticklebacks (*Gasterosteus*). Canadian Journal of Zoology 65:1951–1955.

Roberts, J.A. & G.W. Uetz. 2005. Information content of female chemical signals in the wolf spider, *Schizocosa ocreata*: male discrimination of reproductive state and receptivity. Animal Behaviour 70:217–223.

Roberts, J.A., E. Galbraith, J. Milliser, P.W. Taylor & G.W. Uetz. 2006. Absence of social facilitation of courtship in the wolf spider, *Schizocosa ocreata* (Araneae: Lycosidae). Acta Ethologica 9:71–77.

Rovner, J.S. 1968. An analysis of display in the lycosid spider *Lycosa rabida* Walckenaer. Animal Behaviour 16:358–369.

Rovner, J.S. 1996. Conspecific interactions in the lycosid spider *Rabidosa rabida*: the roles of different senses. Journal of Arachnology 24:16–23.

Rowell, G.A. & W.H. Cade. 1993. Simulation of alternative male reproductive behavior: calling and satellite behavior in field crickets. Ecological Modeling 65:265–280.

Rypstra, A.L., C. Wieg, S.E. Walker & M.H. Persons. 2003. Mutual mate assessment in wolf spiders: Differences in the cues used by males and females. Ethology 109:315–325.

Sadowski, J.A., J.L. Grace & A.J. Moore. 2002. Complex courtship behavior in the striped ground cricket, *Allonemobius socius* (Orthoptera: Gryllidae): Does social environment affect male and female behavior? Journal of Insect Behavior 15:69–84.

Sato, Y., M.W. Sabelis & M. Egas. 2014. Alternative mating behavior in the two-spotted spider mite: dependence on age and density. Animal Behaviour 92:125–131.

Scheffer, S.J., G.W. Uetz & G.E. Stratton. 1996. Sexual selection, male morphology, and the efficacy of courtship signaling in two wolf spiders (Araneae: Lycosidae). Behavioral Ecology and Sociobiology 38:17–23.

Schneider, J.M., M.E. Herberstein, F.C. De Crespigny, S. Ramamurthy & M.A. Elgar. 2000. Sperm competition and small size advantage for males of the golden orb-web spider *Nephila edulis*. Journal of Evolutionary Biology 13:939–946.

Shamble, P.S., D.J. Wilgers, K.A. Swoboda & E.A. Hebets. 2009. Courtship effort is a better predictor of mating success than ornamentation for male wolf spiders. Behavioral Ecology 20:1242–1251.

Shuster, S.M. & M.J. Wade. 2003. Mating Systems and Strategies. Princeton University Press. Princeton.

Snow, L.S.E. & M.C.B. Andrade. 2005. Multiple sperm storage organs facilitate female control of paternity. Proceedings of the Royal Society B 272:1139–1144.

Snow, L.S.E., A. Abdel-Mesih & M.C.B. Andrade. 2006. Broken copulatory organs are low cost adaptations to sperm competition in redback spiders. Ethology 112:1–11.

Stoltz, J.A., D.O. Elias & M.C.B. Andrade. 2008. Females reward courtship by competing males in a cannibalistic spider. Behavioral Ecology and Sociobiology 62:689–697.

Stoltz, J.A., D.O. Elias & M.C.B. Andrade. 2009. Male courtship effort determines female response to competing rivals in redback spiders. Animal Behaviour 77:79–85.

Stoltz, J.A., J.N. McNeil & M.C.B. Andrade. 2007. Males assess chemical signals to discriminate just-mated females from virgins in redback spiders. Animal Behaviour 74:1669–1674.

Taborsky, M., R.F. Oliveira & H.J. Brockmann. 2008. The evolution of alternative reproductive tactics: concepts and questions. Pp. 1–22. *In* Alternative Reproductive Tactics: An Integrative Approach. (R. F. Oliveira, M. Taborsky, H. J. Brockmann, eds.). Cambridge University Press. Cambridge, United Kingdom.

Tietjen, W.J. 1977. Dragline-following by male lycosid spiders. Psyche 84:165–178.

Uetz, G.W., W.J. McClintock, D. Miller, E.I. Smith & K.K. Cook. 1996. Limb regeneration and subsequent asymmetry in a male secondary sexual character influences sexual selection in wolf spiders. Behavioral Ecology and Sociobiology 38:253–257.

Useta, G., B.A. Huber & F.G. Costa. 2007. Spermathecal morphology and sperm dynamics in the female *Schizocosa malitiosa* (Araneae: Lycosidae). European Journal of Entomology 104:777–785.

Wagner Jr., W.E. 1992. Deceptive or honest signaling of fighting ability? A test of alternative hypotheses for the function of changes in call dominant frequency by male cricket frogs. Animal Behaviour 44:449–462.

Watson, P.J. 1991. Multiple paternity as genetic bet-hedging in female sierra dome spiders, *Linyphia litigiosa* (Linyphiidae). Animal Behaviour 41:343–360.

Welke, K. & J.M. Schneider. 2009. Inbreeding avoidance through cryptic female choice in the cannibalistic orb-web spider *Argiope lobata*. Behavioral Ecology 20:1056–1062.

Whitehouse, M.E.A. 1991. To mate or fight? Male-male competition and alternative mating strategies in *Argyrodes antipodiana* (Theridiidae, Araneae). Behavioural Processes 23:163–172.

Wilgers, D.J. & E.A. Hebets. 2011. Complex courtship displays facilitate male reproductive success and plasticity in signaling across variable environments. Current Zoology 57:175–186.

Wilgers, D.J., A.C. Nicholas, D.H. Reed, G.E. Stratton & E.A. Hebets. 2009. Condition-dependent alternative mating tactics in a sexually cannibalistic wolf spider. Behavioral Ecology 20:891–900.

Wilgers, D.J., D. Wickwire & E.A. Hebets. 2014. Detection of predator cues alters mating tactics in male wolf spiders. Behaviour 151:573–590.

Wong, B.B.M. 2004. Male competition is disruptive to courtship in the Pacific blue-eye. Journal of Fish Biology 65:333–341.

Manuscript received 17 December 2015, revised 17 June 2016.