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Dustin J. Wilgers

University of Nebraska-Lincoln, wilgers.spider@gmail.com

Amy C. Nicholas

University of Mississippi

David H. Reed

University of Mississippi

Gail E. Stratton

University of Mississippi

Eileen Hebets

University of Nebraska - Lincoln, ehebets2@unl.edu

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Condition-dependent alternative mating tactics in a sexually cannibalistic wolf spider

Dustin J. Wilgers,¹ Amy C. Nicholas,² David H. Reed,² Gail E. Stratton,² and Eileen A. Hebets¹

1. School of Biological Sciences, University of Nebraska–Lincoln, Lincoln, 348 Manter Hall, NE 68588, USA

2. Department of Biology, University of Mississippi, P.O. Box 1848, University, MS 38677, USA

Corresponding author – D. J. Wilgers, email wilgers.spider@gmail.com

Abstract

Condition-dependent male mating tactics often involve high-quality males capitalizing on the outcome of intersexual selection, whereas low-quality males use behaviors that circumvent female choice to achieve copulation. In the wolf spider *Rabidosia punctulata*, males display 2 distinct mating tactics: 1) “courtship”—consisting of visual and seismic components or 2) “direct mount”—consisting of males grappling/holding females until they assume a copulatory posture. We tested for condition-dependent tactic expression using both field-collected individuals (representing natural variation in body mass and condition) and individuals whose diet we manipulated in the laboratory (representing extreme divergences in body size and condition). Across both natural and diet manipulated individuals, mating tactic was found to be condition dependent; however, the pattern of tactic expression was initially unexpected. Larger males with better body condition primarily adopted a direct mount tactic, whereas smaller males with poorer body condition primarily utilized courtship. Across all males, copulation success tended to be greatest for the direct mount tactic. We suggest that small, poor condition males predominantly utilize the less-successful mating tactic (courtship) in part due to their increased susceptibility to female cannibalism when attempting a direct mount.

Keywords: courtship, Lycosidae, mate assessment, mating systems, *Rabidosia punctulata*

Evolutionary interests regarding reproduction have diverged between the sexes. Although males look to maximize reproductive success through mating with more females, females benefit from mating with only the highest quality males (Andersson 1994; Arnqvist and Rowe 2005). This difference of interests between the sexes can lead to intense intersexual selection (e.g., female choice). Females can use a variety of means (direct or indirect) to accurately assess potential suitors and depending on the distribution of male quality, female choice can result in highly variable male reproductive success (Andersson 1994). Given variable male reproductive success, some individuals may benefit by engaging in alternative mating tactics. Expressed alternative mating tactics can be conditional strategies that allow males to respond adaptively to variation in both extrinsic (e.g., population density, operational sex ratio, habitat heterogeneity, etc.), and intrinsic (e.g., body size, physical condition, age, etc.) factors in their local mating environment (reviews in Gross 1996; Brockman 2001; Shuster and Wade 2003). Alternative mating tactics are widespread across animal taxa (review in Shuster and Wade 2003), including spiders (e.g., Jackson 1982; Lubin 1986; Schmitt et al. 1992; Taylor and Jackson 1999; review in Christenson 1984). Many systems are known to have condition-dependent tactics (e.g., size, physical condition; reviews in Dominey 1984; Gross 1996; Choe and Crespi 1997), and several studies have determined that mating tactics in spiders are dependent on some aspect of male condition (e.g., Christenson and Goist 1979; Rubenstein 1987; Nielsen and Toft 1990; Whitehouse 1991; Schneider et al. 2000; Bel-Venner and Venner 2006; Elgar and Jones 2008; Stoltz et al. 2008).

Condition-dependent alternative male mating tactics are often expressed as a dichotomy based on some aspect of male quality or condition. With reference to female choice, tactics are often dichotomized to enhance or hinder female assessment. During any interactions (inter or intrasexual), individuals can assess each other either directly, for example, via phys-

ical contact or indirectly, via signals or cues (Andersson 1994). Females commonly rely on indirect assessment of males via costly traits or behaviors (e.g., courtship displays—Ryan 1988; Watson and Lighton 1994; Cordts and Partridge 1996; Kotiaho 2000). Many studies, across numerous taxonomic groups, have documented a positive correlation between aspects of male courtship behavior and reproductive success (e.g., birds—Dearborn et al. 2005; fish—Knapp and Kovach 1991; reptiles—Stapley 2008; spiders—Delaney et al. 2007). Given condition-dependent alternative mating tactics then, we might expect good condition males to adopt a tactic that capitalizes on the outcome of intersexual selection by subjecting themselves to assessment (potentially via courtship). In contrast, poor condition males might attempt to reduce the accuracy of female assessment or avoid female assessment altogether (Dawkins 1980; Belovsky et al. 1996).

Males of different species display a variety of alternative mating tactics, which seemingly reduce female assessment (Shuster and Wade 2003). Poor condition males commonly reduce or remove female assessment by either sneaking copulations with unsuspecting females (reviews in Dominey 1984; Gross 1996) or coercing females to copulate through physical force or harassment (e.g., Thornhill 1980; Thornhill and Alcock 1983; review in Clutton-Brock and Parker 1995; Sakaluk et al. 1995; Belovsky et al. 1996). Regardless of the specific form, selection should have molded mating tactics to maximize a male's benefits (i.e., reproductive success) while minimizing associated costs. In sexually cannibalistic species, the cost of a mating attempt can be death. The influence of this potential source of mortality on mating systems has received significant attention (review in Elgar 1992). Sexual cannibalism intensifies the degree of intersexual conflict (Schneider and Lubin 1998), likely influencing the evolution of male mating behaviors (e.g., Fromhage and Schneider 2005) and mating tactics (e.g., Jackson 1980; Rubenstein 1987; Stoltz et al. 2008), potentially resulting in nonintuitive mating tactic expressions.

Wolf spiders (family Lycosidae) are both sexually cannibalistic (e.g., Samu et al. 1999; Persons and Uetz 2005; Vanden Borre et al. 2006) and many species possess elaborate and diverse courtship displays (Miller et al. 1998; Hebets and Uetz 1999, 2000; Stratton 2005; Framenau and Hebets 2007), making them an ideal group for studying the evolution of mating behavior. Because of the potential for sexual cannibalism, the selection pressure exerted on males should be extremely strong and numerous studies on lycosids (primarily in genus *Schizocosa*) have found condition-dependent expression in both male ornamentation (Uetz et al. 2002; Hebets et al. 2008; Shamble et al. in review) and courtship behaviors (Kotiaho 2000; Rivero et al. 2000; Ahtainen et al. 2004; Gibson and Uetz 2007). Condition-dependent trait expression coincides with corresponding female preferences for larger ornamentation and better-conditioned mates (McClintock and Uetz 1996; Scheffer et al. 1996; Hebets and Uetz 2000; Gibson and Uetz 2007; Hebets et al. 2008). To date, most research on wolf spiders indicates mating systems driven by intense intersexual selection and until recently, the use of alternative mating tactics had not been documented.

We recently discovered alternative mating tactics in the grass-dwelling wolf spider *Rabidosia punctulata* (Nicholas 2007). In this relatively large species, males are typically smaller than females (average cephalothorax width: females \bar{x} = 4.99 mm, males \bar{x} = 4.60 mm; from Brady and McKinley 1994) and they possess no secondary sexual characters (e.g., no foreleg ornamentation). When paired with a female, male *R. punctulata* adopt 1 of 2 distinct mating tactics: 1) "courtship" – consisting of visual (foreleg waves) and seismic components or 2) "direct mount" – consisting of males grappling/holding females until they assume a copulatory posture (see supplemental video). During direct mounts, males often grab a female and immediately flip onto their back, which may limit the female's ability to resist copulation (Nicholas 2007). Occasionally (~23% of the time), males use a mixed tactic, where males attempt both direct mounts and courtship in sequence.

Here, we explore the condition dependence of the alternative male mating tactic expression in the sexually cannibalistic wolf spider *R. punctulata*. We test for condition dependence using both 1) mating trials with naturally occurring male and female phenotypes and 2) mating trials with individuals placed on diet manipulations in order to diverge male size and body condition.

Materials and Methods

This study takes advantage of 2 independent data sets – one involving a study using the natural range of male-female phenotypes from a population of *R. punctulata* in Mississippi and a second involving diet manipulations from field-collected individuals in Nebraska. Due to the independent nature of these 2 experiments, there are subtle variations in design as outlined below.

Natural variation experiment

In order to examine condition-dependent mating tactic expression in naturally occurring male and female phenotypes, 200 *R. punctulata* were collected from a single site at the University of Mississippi Field Station (34°25.467'N; 089°23.593'W) in September of 2005. All spiders were collected just prior to their final molt to maturation (\bar{x} = 9 days) to ensure virginity while allowing individuals to maintain their approximate field-based size. Spiders were brought into the laboratory and maintained individually in clear, plastic containers (114 mm × 86 mm × 102 mm) until adulthood. In each container, broomsedge (*Andropogon virginicus*) stems were provided as

a substrate for spiders to molt from and climb on. At maturation, each spider was fed one body-size matched cricket per week. All crickets were supplemented with TetraMin (Blacksburg, VA) fish flakes. An automated lighting system was programmed to mirror a natural light regime (on average 12:12 h light:dark) and temperature ranged between 22 and 26 °C.

All males and females used in mating trials were at least 14 days postmaturation to ensure sexual receptivity (males: \bar{x} = 22.96 ± 0.83 days, range = 15–37; females: \bar{x} = 22.83 ± 0.62 days, range = 16–39). Preliminary experiments suggested that female receptivity begins approximately 12–14 days postmaturation molt. Twelve hours prior to mating trials, both females and males were given one cricket ~1 cm in length to standardize hunger levels and control for motivation and females were placed into their circular plastic mating arenas (diameter = 26 cm; height = 9 cm; lined with filter paper). During the 12-h acclimation period, females deposited pheromone-laden silk, which stimulates male courtship. At the start of a trial, a male was introduced into the arena under a clear plastic vial at the opposite end from the female. Once both spiders were still, the vial was slowly lifted. Trials lasted 20 min and the following behaviors were recorded real time: male mating tactic, male attempted mounts, female receptivity displays, female attacks, premating sexual cannibalism, copulation, and latency to copulation. For males that courted, we also recorded the number of male foreleg waves. No individual was used more than once.

Diet manipulation experiment

In order to artificially diverge male body condition, 216 immature spiders were collected in late July–early August 2007 from Lancaster Co., Nebraska (40°44'57.1"N; 96°49'3.78"W). On average, males were 1.6 molts away from maturity, whereas females were 2.0 molts away. After collection, spiders were housed individually in clear plastic containers (84 mm × 84 mm × 110 mm) with masking tape around the outside to prevent visual contact with neighbors. Individuals were housed in a climate-controlled environment (27 °C) under a 15:9 h light:dark cycle and were randomly assigned 1 of 2 diet treatments for the duration of the experiment: 1) High Quantity (high) – spiders were fed 2 body-size matched crickets twice per week, and 2) Low Quantity (low) – spiders were fed 2 body-size matched crickets once every 2 weeks. Crickets were matched to approximately equal the spider's cephalothorax/prosoma length and all crickets were supplemented with TetraMin (Blacksburg, VA) fish flakes and Fluker's (Port Allen, LA) cricket feed. Because spiders cannot be sexed prior to their penultimate stage (1 molt before maturity), all individuals (males and females) were placed on diet manipulations. Spiders were provided with water *ad libitum* and individuals were checked for molts every 2–3 days to determine the time of maturity.

As in the natural variation mate choice trials, a single female was randomly paired with a single male in mate choice trials and individuals were used only once. Because female mating behaviors (receptivity, cannibalism) are highly influenced by age in some wolf spider species (Uetz and Norton 2007), females were separated into 2 age classes to allow us to examine female age as a factor: 1) young – 12–14 days postmaturation molt and 2) old – 19–21 days postmaturation molt. Because females matured much later than males, we were unable to control for male age, which varied from 14 to 87 days old across trials. However, male ages were similar between diet treatments (high: N = 40, \bar{x} = 42.1 ± 2.9 days, low: N = 42, \bar{x} = 43.4 ± 2.8 days; t_{80} = 0.33, P = 0.74). In order to control for mating motivation, both males and females were fed one small cricket (half the spider's cephalothorax length, ~3 mm) 12–24 h before each trial. Females were placed into circular

plastic trial arenas (diameter = 20.2 cm, height = 7.3 cm) lined with filter paper for at least 1 hr before the trial start, again, allowing time for female acclimation and pheromone deposition. The plastic arenas were surrounded with white visual barriers to minimize disturbances by the observer.

At the start of a trial, a clear plastic vial was placed over the female while the male was introduced into the arena. Males were allowed to acclimate for up to a minute before the female was released. Trials lasted a maximum of 45 min, during which time we recorded the following behaviors: male mating tactic, male attempted direct mounts (i.e., female successfully ejected male), female attacks, premating sexual cannibalism, copulation success, and latency to copulation. Again, if males courted, we recorded the latency to first courtship and the number of male foreleg waves.

Phenotypic measurements

For all spiders, we took 2 measures of body size: cephalothorax width and mass. Because an arthropod's exoskeleton is fixed between molts and on final maturation, cephalothorax width provides a static body-size measurement. In contrast, body mass can fluctuate dramatically with recent foraging history, providing a more dynamic measure of body size. For spiders used in the "natural variation" mating trials, mature spiders were gently restrained with clear film and placed on top of a sponge underneath a dissecting microscope. An ocular micrometer was used to measure cephalothorax width in mm. For the individuals used in the diet manipulation experiment, cephalothorax width was measured 3 times per mature individual with digital calipers. Measurements were taken to the nearest 0.01 mm and then averaged across the 3 measurements. To obtain body mass for both experiments, all individuals were weighed to the nearest milligram (Natural Variation: Sartorius Basic Model BA110S; Diet Manipulation: Ohaus Adventurer Pro AV64) prior to each mating trial. An additional measure of body mass was taken for the diet manipulated individuals—maturation mass was obtained within 2 days post final maturation molt to assess the efficacy of our diet manipulations.

Body conditions were calculated using the residuals of a regression of body mass on cephalothorax width (Jakob et al. 1996). Both mass and cephalothorax width were natural log transformed (Kotiaho 1999). Residuals were calculated using regression for each population separately (MS—natural variation trials and NE—diet manipulation trials). In addition, separate regressions were used for each sex within the 2 populations due to the considerable sexual size dimorphism (SSD).

Statistical analysis

To decrease the repetitive nature of our results, in analyzing tactic-specific copulation success and cannibalism frequencies, only analyses from the diet manipulation experiment are presented. However, the findings are the same from the natural variation experiment. Additionally, because body size and mass are highly correlated ($N = 195$, $r^2 = 0.75$, $P < 0.001$), we report only mass as an independent variable.

All statistical analyses were performed in JMP IN (version 5.1.2, SAS Institute, Inc.). If data failed normality, nonparametric analyses were used. Results are reported as mean \pm standard error (SE).

Results

Natural variation experiment

Mating tactic expression

Both pure mating tactics (courtship and direct mount) and mixed tactics were observed during the mating trials ($N =$

92), but the frequency of tactic expression varied across trials (Likelihood ratio, $\chi^2_2 = 15.3$, $P < 0.001$; Figure 1A-I). The majority of males (73%) adopted a pure tactic (courtship: 52%, direct mount: 21%), whereas fewer males used a mixed tactic (27%). All males using the mixed tactic first attempted a direct mount and subsequently switched to courtship.

Male mating tactic expression (courtship, mixed, direct mount) varied with body mass (courtship: $N = 48$, $\bar{x} = 0.246 \pm 0.007$ g; mixed: $N = 25$, $\bar{x} = 0.271 \pm 0.009$ g; direct mount: $N = 19$, $\bar{x} = 0.27 \pm 0.011$ g; ANOVA, $F_{2,91} = 3.04$, $P = 0.05$) and body condition ($F_{2,91} = 6.74$, $P = 0.002$; Figure 2). Males using the direct mount and mixed tactics were larger and in overall better body condition than males using courtship (Figure 2). Female body mass and condition were not different across the expressed male mating tactics (mass: Kruskal-Wallis test, $\chi^2_2 = 2.21$, $P = 0.33$; condition: $F_{2,91} = 1.63$, $P = 0.20$).

Although male mass and body condition correlated with mating tactic expression, this could be due in part (or solely) to male size relative to female size (i.e., SSD = female mass/male mass). Although trial SSD measures varied across mating tactics (ANOVA, $F_{2,91} = 5.56$, $P = 0.005$), trial SSD significantly differed ($P < 0.05$, Tukey post hoc comparisons) only between the mixed and courtship tactics (courtship: $\bar{x} = 1.77 \pm 0.06$; mixed: $\bar{x} = 1.42 \pm 0.09$; direct mount: $\bar{x} = 1.54 \pm 0.10$). We used a logistic regression model to identify which characters (male mass, male condition, and trial SSD) were important in mating tactic expression. We found male condition was the only significant predictor; however, trial SSD approached significance with little difference in predictive power compared with male condition (Likelihood ratio; male mass: $\chi^2_2 = 0.33$, $P = 0.84$; male condition: $\chi^2_2 = 7.82$, $P = 0.02$; trial SSD: $\chi^2_2 = 5.62$, $P = 0.06$).

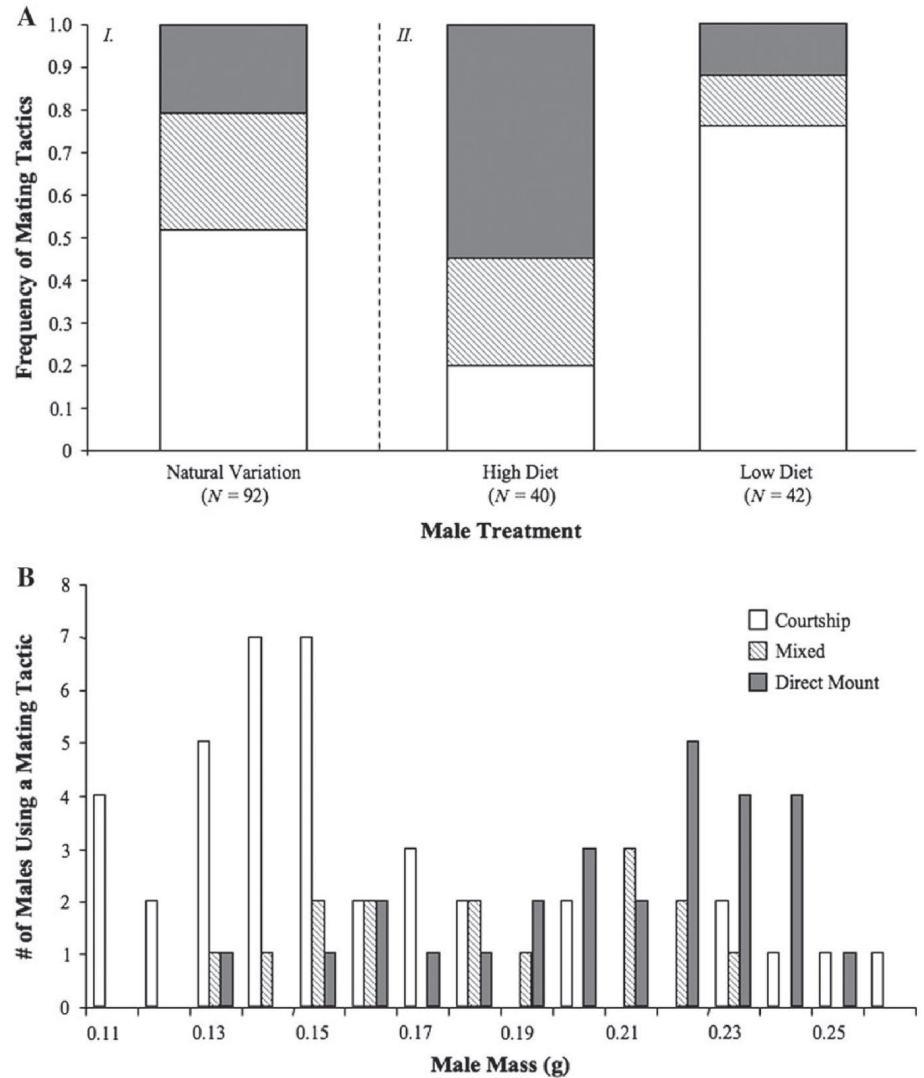
Diet manipulation experiment

Our diet manipulations successfully diverged the body mass, size, and condition of our 2 treatment groups. On collection, all spiders were similar in mass across diet treatments (males: Wilcoxon 2-sample test, $Z = 1.05$, $P = 0.29$; females: Wilcoxon 2-sample test, $Z = 1.4$, $P = 0.16$). However, at maturation, we found significant differences between diet manipulations for both males and females in body size, mass, and condition (Table 1), with high-diet individuals being approximately 12% larger in body size (males = 12%, females 11%), 33% heavier (males = 35%, females = 32%) and in better condition.

Mating tactic expression

During mating trials ($N = 82$), individuals from both low- and high-diet groups exhibited both pure mating tactics (courtship: 49%, direct mount: 33%), whereas some individuals (18%) used a mixture of tactics. These tactic frequencies were similar to those witnessed in the natural variation experiment (Likelihood ratio, $\chi^2_2 = 4.08$, $P = 0.13$). Of the males using the mixed tactic, 73% (11/15) used a direct mount first, whereas 27% (4/15) began with courtship. The frequency of tactics expressed was dependent on the male diet treatment (Figure 1A-II), but not female diet treatment or the interaction between male and female diet treatment (Likelihood ratio; male diet: $\chi^2_1 = 26.16$, $P < 0.001$; female diet: $\chi^2_2 = 2.03$, $P = 0.15$; male*female diet: $\chi^2_2 = 0.35$, $P = 0.56$). High-diet males were nearly 3 times as likely to use the direct mount tactic compared with the courtship tactic, whereas low-diet males were more than 6 times as likely to use the courtship tactic compared with the direct mount tactic (Figure 1A-II). Male age (# days postmaturity) did not differ between diet treatments (Wilcoxon 2-sample test, $Z = 0.21$, $P = 0.83$) or between expressed mating tactics (Kruskal-Wallis test, $\chi^2_2 = 3.43$, $P = 0.18$). Female age class did not influence the expression of male tactics (Likelihood ratio, $\chi^2_2 = 1.12$, $P = 0.57$).

Figure 1. (A) I. Frequency of alternative mating tactics in male *Rabidosa punctulata* across natural variation in male size. The natural frequencies of expressed tactics were not even ($P < 0.001$), with the majority of males using courtship. II. Frequency of alternative mating tactics based on the diet manipulation studies. Males exhibited condition-dependent frequencies of different alternative mating tactics ($P < 0.001$). High-condition males were twice as likely to exhibit the direct mount tactic compared with courtship, whereas low-condition males were 6 times more likely to court rather than use the direct mount tactic. (B) Distributions of male mating tactics based on body mass from the diet manipulation study.



The distributions of males using the pure tactics differed with regards to male mass, whereas males using the mixed tactic tended to be intermediate (Kruskal-Wallis test, $\chi^2_2 = 21.89$, $P < 0.001$; Figure 1B). Within the diet treatments, body mass was significantly different among tactics for low-diet males (Kruskal-Wallis test, $\chi^2_2 = 5.86$, $P = 0.05$) with individuals using the direct mount and mixed tactic being heavier

than males using the courtship tactic (courtship: $N = 31$, $\bar{x} = 0.14 \pm 0.004$ g; mixed: $N = 5$, $\bar{x} = 0.16 \pm 0.009$ g, direct mount: $N = 5$, $\bar{x} = 0.17 \pm 0.009$ g); although within high-diet males, body mass was similar across tactics (Kruskal-Wallis test, $\chi^2_2 = 4.43$, $P = 0.11$).

Table 1. Influences of diet quantity manipulations on body measurements of female and male *Rabidosa punctulata*

Sex	Diet	N	Size (mm)	Mass (g)	Condition
Female	High	50	4.76 ± 0.04	0.25 ± 0.01	0.05 ± 0.01
	Low	41	4.22 ± 0.05	0.17 ± 0.01	-0.06 ± 0.02
			($P < 0.001$)*	($P < 0.001$)*	($P < 0.001$ **)
Male	High	50	4.54 ± 0.04	0.20 ± 0.003	0.04 ± 0.02
	Low	53	3.99 ± 0.04	0.13 ± 0.003	-0.04 ± 0.02
			($P < 0.001$)*	($P < 0.001$)*	($P < 0.001$ **)

Body measurements reported as means ± SE.

Females were significantly larger than males in both size (Wilcoxon 2-sample test, $Z = 4.15$, $P < 0.001$) and mass at maturation (Wilcoxon 2-sample test, $Z = 6.12$, $P < 0.001$).

* Wilcoxon 2-sample test of high versus low-diet individuals.

** *t*-test of high- versus low-diet individuals.

When modeling mating tactic as a function of a male's diet treatment and trial SSD, our logistic regression model indicated that male diet treatment alone is sufficient to predict male mating tactic (Likelihood ratio; male diet: treatment $\chi^2_1 = 16.95$, $P < 0.001$; trial SSD: $\chi^2_1 = 0.87$, $P = 0.65$). In order to determine a potential switch point between the pure tactics, we used a logistic regression to predict male mating tactic (courtship vs. direct mount) as a function of the mass of males and females, and the interaction between the 2. Male mass was the only significant predictor of mating tactic expression (Likelihood ratio; male mass: $\chi^2_1 = 20.0$, $P < 0.001$; female mass: $\chi^2_1 = 0.002$, $P = 0.96$; male*female mass: $\chi^2_1 = 0.07$, $P = 0.80$). The logistic regression model predicted the mating tactic switch point based on male mass to be 0.196 g (Figure 3-I). This indicates that males above this mass are more likely to use the direct mount tactic, whereas males below this mass are more likely to use courtship, regardless of female mass or male mass relative to the female (SSD). Males close to this switch point may be more likely to switch tactics within a trial (mixed tactic), and in fact this switch point falls in the range

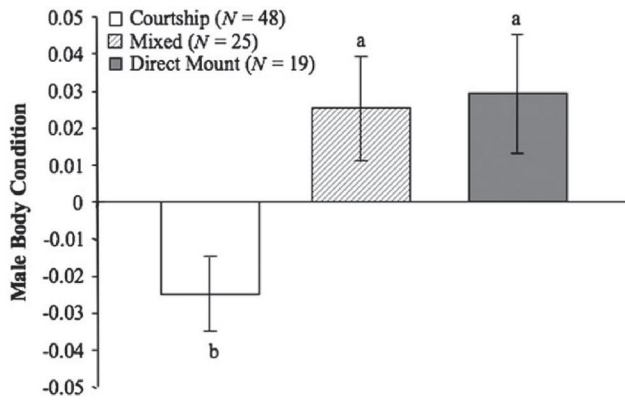


Figure 2. Body condition indices across mating tactics from natural variation experiment. Body condition was calculated using the residuals of a regression of body mass (g) on body size (cephalothorax width, mm). Both body mass and body size were natural log transformed. Positive values indicate better body condition than average (controlling for size), whereas negative values indicate poorer body condition than average. Male body condition was significantly different between mating tactics expressed ($P = 0.002$). Mating tactics sharing the same letter are not significantly different as indicated by post hoc Tukey-Kramer pairwise comparisons ($P < 0.05$).

of masses for males adopting the mixed tactic ($\bar{x} = 0.181 \pm 0.033$ g, Figure 3-II).

Mating tactic success

Males utilizing the different mating tactics experienced different copulation success, although these differences were marginally insignificant (Likelihood ratio, $\chi^2_2 = 4.74$, $P = 0.09$, Figure 4a-II), which is similar to the findings of the natural variation experiment (Likelihood ratio, $\chi^2_2 = 5.72$, $P = 0.06$; Figure 4a-I). Overall, males using the direct mount tactic tended to be the most successful at gaining copulations, and when comparing just the pure tactics, copulation rate was significantly greater with a direct mount than courtship (Likelihood ratio, $\chi^2_1 = 4.65$, $P = 0.03$, Figure 4a-II). Within the mixed tac-

tic, male copulation success varied with which tactic was used first. Males using courtship first ($N = 4$, 100% copulation rate) were more likely to copulate than males that used a direct mount first ($N = 11$, 27% copulation rate; Likelihood ratio, $\chi^2_1 = 7.84$, $P = 0.005$). Copulation success rates were influenced by male diet (Likelihood ratio, $\chi^2_1 = 7.13$, $P = 0.008$), favoring high-diet males (Figure 4a-II). Female diet treatment and age class did not have an influence on copulation rate (diet: Likelihood ratio, $\chi^2_1 = 1.82$, $P = 0.18$; age class: Likelihood ratio, $\chi^2_1 = 0.05$, $P = 0.82$).

Latency to copulation from the start of the trial was also significantly different across expressed tactics (Kruskal-Wallis test, $\chi^2_2 = 15.11$, $P < 0.001$; Figure 4b). Males utilizing the direct mount tactic procured copulations significantly faster than either courtship (Wilcoxon 2-sample test, $Z = 3.57$, $P < 0.001$) or mixed tactics (Wilcoxon 2-sample test, $Z = 2.57$, $P = 0.01$). However, latency to copulation was the same for courtship and mixed tactics (Wilcoxon 2-sample test, $Z = 0.63$, $P = 0.5$; Figure 4b). This same pattern held even when recalculating copulation latency for the courtship tactic from the start of courtship (courtship: $N = 16$, $\bar{x} = 552.9 \pm 80.8$ s; direct mount: $N = 18$, $\bar{x} = 215.7 \pm 76.2$ s; Wilcoxon 2-sample test, $Z = 2.81$, $P = 0.005$).

In testing for tactic-specific predictors of copulation success, we found no differences in male body measurements (mass, condition) for successful versus unsuccessful males using either the direct mount or mixed tactic (Table 2). However, within the courtship tactic, successful males tended to be heavier than unsuccessful males, while condition did not seem to influence copulation success (Table 2). Furthermore, females mated with high-diet courting males significantly more often than low-diet courting males (Likelihood ratio, $\chi^2_2 = 5.1$, $P = 0.02$; Figure 4A-II). Trial SSD only influenced tactic-specific copulation success in males using courtship, where successful males tended to be heavier relative to the female (Table 2).

In analyzing male courtship, we found that high-diet males tended to court more intensely (# courtships/s) than low-diet males, but this difference was marginally insignificant (high: $N = 8$, $\bar{x} = 0.04 \pm 0.009$ #/s; low: $N = 32$, $\bar{x} = 0.02 \pm 0.004$ #/s; Wilcoxon 2-sample test, $Z = 1.80$, $P = 0.07$). For the mixed tac-

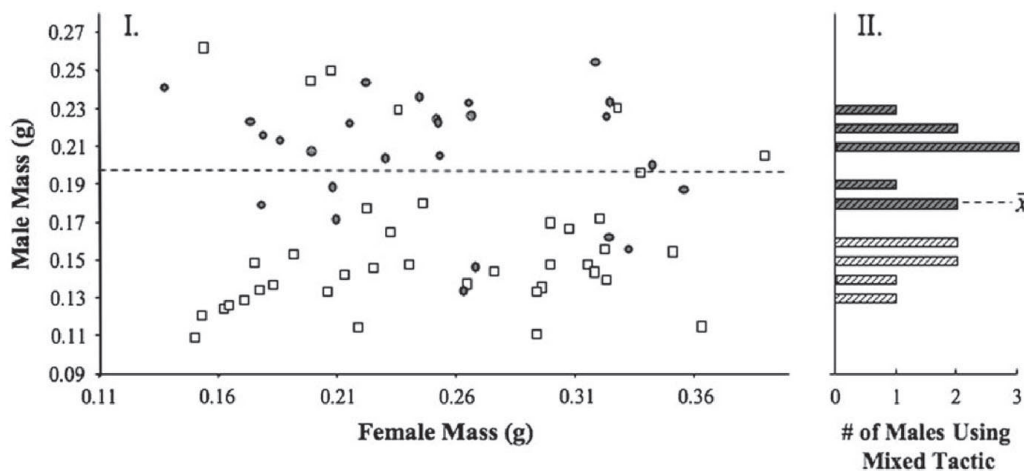
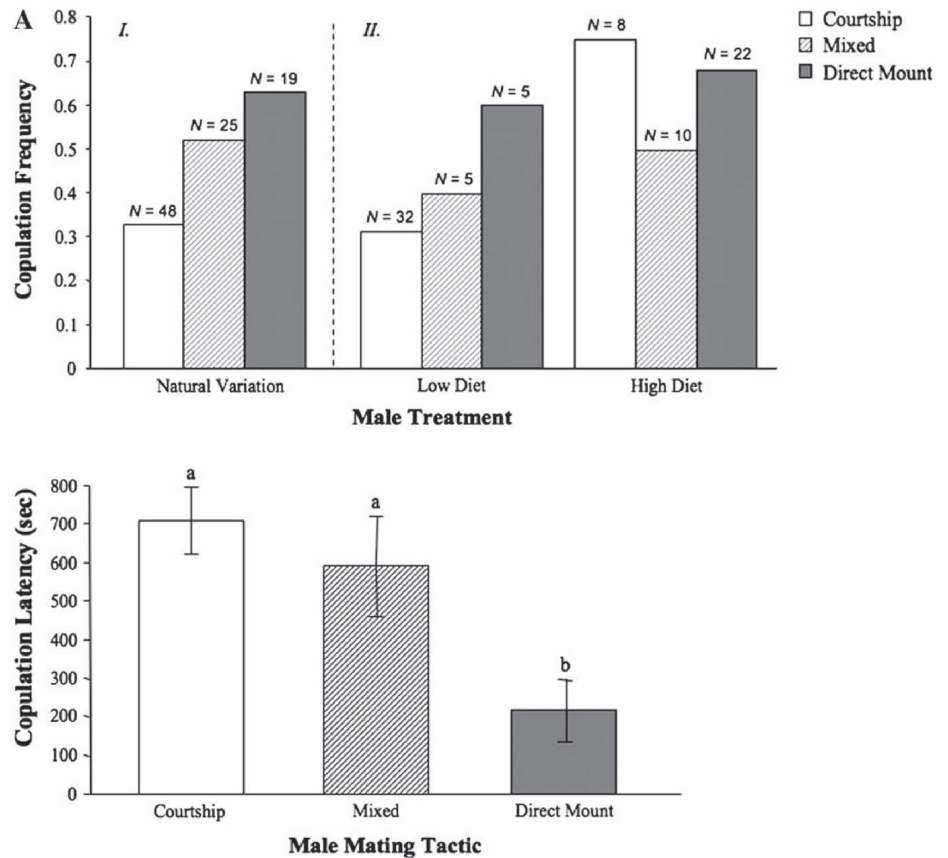


Figure 3. (I) Distribution of male mating tactics as a function of male and female mass. Each point represents the mating tactic used (direct mount: gray circle; courtship: open square) during a given mating trial. The dashed line represents the predicted mating tactic switch point between pure tactics (direct mount–courtship) for males based on male mass alone, where males above this line are more likely to use direct mounts, and males below are more likely to use courtship. The switch point was calculated from a logistic regression model indicating male mating tactic is predicted by male mass alone (male: $P < 0.001$; female: $P = 0.96$; male*female: $P = 0.8$). (II) Frequency of males using the mixed mating tactic across different male masses. The color of the hatched bars indicates the tactic males used first (direct mount: gray; courtship: white). The mean mass ($\bar{x} = 0.182$ g) for males expressing the mixed tactic is indicated by the dashed line.

Figure 4. (A) Copulation success of different male mating tactics in *R. punctulata* from 2 separate data sets I.) natural variation and II.) diet manipulations. Differences in copulation success across tactics were marginally insignificant for both the natural variation ($P = 0.06$) and diet manipulation experiment ($P = 0.09$). In the diet experiment, overall copulation success was significantly greater for high-diet males compared with low-diet males ($P = 0.008$); however, tactic-specific copulation success was only significantly different between diets for the courtship tactic ($P = 0.02$). (B). Latency to copulation for different male mating tactics from the diet manipulation experiment. Latencies were significantly different across tactics ($P < 0.001$). Copulation latencies were calculated from the start of the trial. Mating tactics sharing the same letter are not significantly different as indicated by post hoc comparisons ($P < 0.05$).



tic, males that used courtship first courted more intensely ($N = 4$, $\bar{x} = 0.03 \pm 0.007$ #/s) than males that used a direct mount first ($N = 11$, $\bar{x} = 0.01 \pm 0.004$ #/s; Wilcoxon 2-sample test, $Z = 2.02$, $P = 0.04$). Courtship intensity was found to influence copulation success, as indicated by significantly higher courtship intensities for successful ($N = 16$, $\bar{x} = 0.04 \pm 0.005$ #/s) versus unsuccessful males ($N = 24$, $\bar{x} = 0.008 \pm 0.004$ #/s; Wilcoxon 2-sample test, $Z = 5.64$, $P < 0.001$). On the contrary, copulation success did not increase with effort in the direct mount tactic.

In fact, unsuccessful males ($N = 9$, $\bar{x} = 4.00 \pm 0.43$) had significantly more mounting attempts than successful males ($N = 18$, $\bar{x} = 0.17 \pm 0.31$; Wilcoxon 2-sample test, $Z = 4.40$, $P < 0.001$). There were no differences in the number of direct mounting attempts between the diet treatments (low: $N = 5$, $\bar{x} = 1.60 \pm 1.02$; high: $N = 22$, $\bar{x} = 1.41 \pm 0.49$; Wilcoxon 2-sample test, $Z = 0.07$, $P = 0.95$) and the number of mounting attempts was not correlated with male mass (Spearman's rank, $N = 27$, $\rho = 0.07$, $P = 0.74$).

Table 2. Differences in body measurements based on copulation success in *Rabidosa punctulata*

Mating tactic	Cop	Mass ^a (N)	Condition ^b (N)	SSD ^c (N)
Courtship	No	0.147 ± 0.008 (24)	-0.02 ± 0.02 (24)	1.80 ± 0.10 (24)
	Yes	0.176 ± 0.010 (15) ($P = 0.06$)*	0.02 ± 0.03 (14) ($P = 0.25$)**	1.44 ± 0.13 (15) ($P = 0.05$)*
Mixed	No	0.19 ± 0.01 (8)	-0.04 ± 0.03 (7)	1.58 ± 0.16 (8)
	Yes	0.17 ± 0.01 (7) ($P = 0.27$)*	-0.03 ± 0.03 (7) ($P = 0.87$)**	1.30 ± 0.17 (7) ($P = 0.33$)*
Direct mount	No	0.20 ± 0.01 (9)	0.03 ± 0.03 (9)	1.40 ± 0.14 (9)
	Yes	0.21 ± 0.01 (18) ($P = 0.33$)*	0.02 ± 0.02 (17) ($P = 0.81$)**	1.19 ± 0.10 (17) ($P = 0.16$)*
Cannibalism ^d	No	0.181 ± 0.005 (75)	0.007 ± 0.01 (72)	1.47 ± 0.06 (74)
	Yes	0.143 ± 0.017 (6) ($P = 0.04$)*	-0.087 ± 0.04 (6) ($P = 0.01$)**	1.72 ± 0.21 (6) ($P = 0.19$)*

* Wilcoxon 2-sample test of difference between copulating and noncopulating or cannibalized and noncannibalized males.

** *t*-Test of difference between copulating and noncopulating or cannibalized and noncannibalized males.

a. Body mass measured at the time of trial (g).

b. Body condition indicated by residuals calculated from regressions of body mass on cephalothorax width (both natural log transformed).

c. Mass SSD reported as the means (\pm SE) of trial ratios (female:male) of mass.

d. Premating cannibalism frequencies were similar across all tactics ($P = 0.82$), reported means (\pm SE) on body measurements for trials in which cannibalism did or did not occur are pooled across mating tactics.

Mating tactic costs

Female aggressive behaviors were relatively common, occurring in 27% of trials ($N = 82$). The probability of a female attack varied across both male diet treatment (Likelihood ratio, $\chi^2_2 = 5.7$, $P = 0.02$) and mating tactic (Likelihood ratio, $\chi^2_2 = 7.1$, $P = 0.03$). Low-diet males were 2.5 times more likely to be attacked than high-diet males (low diet: 16/42; high diet: 6/40), whereas males that used courtship were nearly 3 times more likely to be attacked than males using other tactics (courtship: 40% [16/40]; mixed: 13.3% [2/15]; direct mount: 14.8% [4/27]). Attacks were more often directed toward lighter males (attacked males: $\bar{x} = 0.157 \pm 0.008$ g; nonattacked males: $\bar{x} = 0.186 \pm 0.005$ g; Wilcoxon 2-sample test, $Z = 2.54$, $P = 0.01$) and males with lower body condition indices (attacked males: $\bar{x} = -0.05 \pm 0.02$; nonattacked males: $\bar{x} = 0.02 \pm 0.01$; $t_{129} = 2.92$, $P = 0.002$). In trials where female attacks occurred ($N = 22$), 27% of the time, the attacks escalated to premating sexual cannibalism. Cannibalism rates were not different across tactics (courtship: 10% (4/40); mixed: 6.7% (1/15); direct mount: 3.7% (1/27); Likelihood ratio, $\chi^2_2 = 1.0$, $P = 0.60$); however, they were dependent on male diet treatment (low diet: 14% (6/42); high diet: 0% (0/40); Likelihood ratio, $\chi^2_1 = 8.5$, $P = 0.004$). Males that were cannibalized were significantly lighter and had significantly lower body condition indices when compared with males not cannibalized (Table 2). Cannibalism rates were not dependent on female diet (Likelihood ratio, $\chi^2_1 = 1.67$, $P = 0.20$) or absolute female body measures (mass: Wilcoxon 2-sample test, $Z = 0.30$, $P = 0.76$; condition: $t_{78} = 0.27$, $P = 0.60$). In addition, mass SSD was not different between pairs in which cannibalism occurred versus did not occur (Table 2). A logistic regression model used to predict the probability of cannibalism indicated male condition and mass as significant (or near significant respectively) predictors of cannibalism (male condition: $\chi^2_1 = 3.78$, $P = 0.05$; male mass: $\chi^2_1 = 3.47$, $P = 0.06$), whereas other factors had little or no predictive power (female mass: $\chi^2_1 = 2.56$, $P = 0.11$; mating tactic: $\chi^2_2 = 0.4$, $P = 0.82$; trial SSD: $\chi^2_1 = 2.32$, $P = 0.13$).

Discussion

Using 2 independent data sets, we establish that the mating tactics used by male *R. punctulata* wolf spiders are indeed condition dependent. Larger males in good condition predominantly utilized a direct mount tactic, which involves males forcefully grabbing and grappling with females until acquiescence and eventual copulation. In contrast, smaller males in poor condition predominantly utilized a courtship tactic. This pattern of condition-dependent mating tactic is robust, as it was observed across geographically separated populations using both naturally occurring phenotypes and diet manipulations. Although we found no specific predictors of mating tactic success based on male body measures, we did find that males using direct mounts tended to experience higher copulation frequencies and shorter latencies to copulation than males using other tactics. Additionally, we found that smaller, poor condition males suffered higher sexual cannibalism rates than larger males in better condition.

A priori, one might have predicted large, good condition males to engage in courtship, as it likely provides a female an indirect measure of condition. However, although direct mounts may appear to remove the variable of female assessment from male reproductive success, it could instead provide the female with a direct measure of male size or condition. Female *R. punctulata* weigh on average 50% more than males, making it unlikely that females lose control over copulations during direct mounts. Due to the physical and in-

termediate nature of this mating tactic, direct mounts may well serve as a direct form of female assessment. By grappling with a male directly, females could gain precise information regarding male size and/or strength. This idea of direct assessment is supported in part by our data indicating that only the largest low-diet males attempted a direct mount. These large low-diet males experienced greater copulation success than low-diet courting males and equal copulation success with high-diet males that used a direct mount. Thus, although large, good condition males may be circumventing indirect assessment, they may instead be opting for direct female assessment.

With respect to copulation success, high-diet males were equally successful when using a courtship tactic as compared to a direct mount tactic. Given seemingly similar benefits, why then do high-diet males preferentially engage in direct mounts? We propose that for large, good condition males, there may be costs associated with courtship that outweigh the benefits, in which case theory predicts reduced courtship (Reynolds 1993). For example, we found the latency to copulation to be significantly shorter for the direct mount tactic than for either of the other mating tactics. If the time invested in courtship is costly, for example by reducing the amount of time available for foraging (Clutton-Brock et al. 1982; Wolff and Van Horn 2003) or by placing individuals at a high risk of predation (reviewed in Kotiaho et al. 1998; Zuk and Kolluru 1998; Herberstein et al. 2002; Roberts et al. 2007), then larger males may avoid these costs by engaging in a direct mount. Predation risk is known to influence mating behaviors (reviewed in Lima and Dill 1990; Sih et al. 1990; Koga et al. 1998), courtship activity (e.g., Taylor et al. 2005), and tactic expression in other systems (e.g., Godin 1995; Oku and Yano 2008). Additionally, prolonged courtship may result in unintentionally attracting other surrounding males (Kiflawi and Gray 2000; Balsby and Dabelsteen 2005), which may decrease an individual's chance of successful copulation (but see Roberts et al. 2006). Regardless of the specifics, courtship clearly carries along with it costs—none of which are similarly found in the direct mount tactic.

In addition to the potential costly time investment and/or increased susceptibility to predation associated with conspicuous courtship, an alternative advantage to a direct mount tactic could relate to variability in the signaling environment. As discussed by Guilford and Dawkins (1991), signal content is meaningless if not successfully detected by the intended receiver. Although the courtship display of *R. punctulata* contains both visual and seismic signals, the signaling environment is extremely complex. *Rabidosia punctulata* lives in prairie habitats composed of numerous disconnected substrates (i.e., blades of grass) with lots of wind, both of which likely reduce the efficacy of signaling in either modality. The successful transmission of seismic and/or visual courtship signals has been shown to be critical for successful mating in other wolf spider taxa (Scheffer et al. 1996; Hebets and Uetz 1999, 2000; Hebets et al. 2006). Variable signal detection across environments has been proposed to drive or maintain the evolution of male polymorphisms (Clark and Uetz 1993; Clark and Biesiadecki 2002; Chunco et al. 2007). In circumstances of reduced courtship efficacy, males could remove variability in female detection and take advantage of their close proximity to a female by attempting a direct mount. The influence of the signaling environment on mating tactic expression certainly warrants further investigation in this system.

In contrast to high-diet males, low-diet males experienced different copulation success across mating tactics. Specifically, low-diet males achieved more copulations using a direct

mount as compared to a courtship tactic, yet low-diet males were more likely to court than engage in a direct mount. As with the high-diet males, there seems to be a disconnect between tactic expression and tactic success. Again, we propose that this discrepancy can be understood when taking costs into account. Although small, poor condition males frequently engage in an arguably less-successful mating tactic, courtship may in fact maximize a male's benefits (i.e., acquiring a copulation) relative to costs (e.g., energetic, time, possibility of death, etc.) as compared to a direct mount tactic. For example, as discussed above, a direct mount may provide a female with a direct assessment of male size or condition, whereas courtship, being indirect, may provide a less accurate assessment. Small males may then benefit by avoiding direct assessments. Alternatively, small males may simply be physically incapable of successfully grappling and holding a larger female for copulation. If this were the case however, we would expect to see a negative correlation between the number of attempted mounts and male size due to numerous unsuccessful attempts by smaller males compared to relatively fewer attempts by large males. Instead, we found no correlation between male size and attempted mounts and no differences in the number of attempted mounts between our low and high-diet males, indicating that this is an unlikely explanation for our results.

Although differential benefits from each tactic to small, poor condition males may explain some of our observed condition-dependent tactic expression, tactic-specific costs may be more insightful given the cannibalistic nature of this species. One obvious cost to any mating attempt in sexually cannibalistic taxa is the potential for total loss of future fitness (i.e., death). Sexual cannibalism is known to be an important selection pressure on male spiders, potentially regulating population-level characteristics, (e.g., male size, condition, ornamentation; Buddle et al. 2003; Persons and Uetz 2005) along with influencing mating behaviors (Elgar and Jones 2008), male mate choice (Gaskett et al. 2004), and the expression of different mating tactics based on relative risk (Jackson 1980; Robinson and Robinson 1980; Foellmer and Fairbairn 2004). In wolf spiders, greater degrees of SSD have been shown to dramatically increase the likelihood of sexual cannibalism (Wilder and Rypstra 2008). Although our observed premating cannibalism rates were relatively low (7%), sexual cannibalism does happen in *R. punctulata*. We suggest that the low observed frequency in these experiments may be the result of satiated females (females were fed shortly before trials) or alternatively past selection on mating tactic expression to reduce the risk of sexual cannibalism. Unfortunately, due to the small number of observed cannibalism events, we lack statistical power to discern if cannibalism rates are tactic-dependent. Nonetheless, despite small sample sizes our data do demonstrate that cannibalized males were significantly smaller than noncannibalized males, suggesting a greater risk of cannibalism to small, small, poor condition individuals.

Courtship behavior has been widely suggested to reduce female predatory behaviors, reducing cannibalistic tendencies (Elgar 1992; Schneider and Lubin 1998). Thus, although small, poor condition males may be at a mating disadvantage compared with large, good condition individuals when using a courtship tactic, it is possible that they are also less likely to be attacked and killed than if they attempted a direct mount—a tactic that brings an already vulnerable male into close contact with a potentially unreceptive female. For small, poor condition male *R. punctulata*, "making the most of a bad situation" may mean courting instead of risking injury or death by attempting to directly mount a female.

Mating tactic expression in *R. punctulata* is plastic, as a single male can alter his tactic both within (i.e., mixed tac-

tic) and between trials (Nicholas 2007; Wilgers DJ, personal observation). Males using the mixed tactic offer an interesting intermediate to compare the distribution of male characteristics and tactic expression. In general, males using the mixed tactic were of similar size and condition to those males using a pure direct mount tactic. In the diet manipulation, the prediction of the tactic switch point based on male mass was similar to the mean mass of those males using both tactics within a trial (mixed). Male copulation success for the mixed depended on which tactic was expressed first. Males attempting a direct mount first, were unsuccessful, and switched to courtship were much less likely to copulate than males that courted first and attempted a direct mount later. Females may assess and reject males using direct mounts based on size or condition. After rejection these males are unable to change females minds with courtship, due to reduced courtship intensity compared with males that begin with courtship, which potentially indicates the energetically costly nature of direct mounts. This potential trade-off could also explain why all males don't initially attempt direct mounts when encountering a female.

In this study, we considered reproductive success as males acquiring a single copulation. Interestingly, female *R. punctulata* have been witnessed to mate multiply (Wilgers DJ, personal observation), opening up the possibility of sperm competition and/or cryptic female choice (Eberhard 1996). Future studies investigating the role of sperm competition and cryptic female choice on tactic-specific fitness will provide further insight into this unique system. In addition, future studies are planned to quantify other tactic-specific fitness measures (e.g., eggsac production, number of spiderlings).

In summary, we have documented a pattern of condition-dependent mating tactic expression in the wolf spider, *R. punctulata*, where large, good condition males predominately use a direct mount mating tactic that forgoes courtship and involves male-female grappling, whereas small, poor condition males engage in courtship. We suggest that the potential for sexual cannibalism makes it risky for small, poor condition males to attempt direct mounts and that the costs of courtship make it beneficial for large, good condition males to attempt direct mounts. The potential for extreme costs due to sexual cannibalism followed by differential fitness benefits from sperm competition in *R. punctulata* adds an interesting component to understanding the evolution of alternative mating tactics and we believe that this system will provide innumerable insights into mating system dynamics in the future.

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Supplemental Video

Video shows a staged mating interaction in *Rabidosa punctulata*, where male performs the direct mount mating tactic. The video was captured on a Fastcam 1024 PCI high-speed digital camera at 500 frames per second. The end of the video was shortened upon the male finishing the mount by crawling onto the females dorsal side to begin copulation.