

The Effects of Male-Male Competition on the Mating Behavior of *Rabidosa punctulata*

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ABSTRACT

Competition among male organisms varies greatly within a species depending on internal as well as external factors. These factors can result in alternative mating tactics used to try to maximize fitness under specific situations. In the wolf spider *Rabidosa punctulata*, males exhibit two distinct mating tactics, each exhibiting its own level of physical risk and reward when related to possible fitness: 1) “courtship”—comprising visual and seismic cues or 2) “direct mount”—involving males grappling females until copulation is successful or they are removed by force. Direct mount carries more physical risk for males, as female wolf spiders are cannibalistic. Individuals were tested for variations in alternative mating tactics in a competitive (experimental) and noncompetitive (control) environment. Results showed no differences in chosen alternative mating tactics among males in either environment, showing that intrasexual selection is not a factor for this species of spider. When combined with the data of a similar study, we can conclude that this is the case because of the previously unknown polygamous nature of the female wolf spider. Males do not have to be the first to copulate, and as such do not have to risk additional physical harm by adopting an alternative mating tactic that may carry more risks.

Keywords: *alternative mating tactics, wolf spider, social environment, intrasexual selection*

INTRODUCTION

Organisms evolve certain traits and features to help them maximize their reproductive success. Within a species, often these traits and behaviors are very diverse and are expressed differently based on variation in factors that are both intrinsic (e.g. physical traits, age) and extrinsic (e.g. predation, competition) to individuals. These alternative mating tactics are often behavioral responses attempting to optimize fitness under condition specific situations (Dominey 1984). It is important to understand the conditions in which one tactic may be preferable over another, which can encompass a wide variety of situations, including the surrounding social environment that may include competing males.

When males are attempting to find a mate, they often find themselves in direct competition with other males in their immediate vicinity. This intrasexual competition has a direct impact on the mating success of males and increases the degree of sexual selection amongst males. Sexual selection in a social context often favors alterations in a male’s behavior that enhance the success of finding a mate. In the horseshoe crab, *Limulus polyphemus*, older males that are in relatively poor health and cannot compete with younger males often adopt the “satellite” tactic in order to fertilize female eggs (Gross 1996). The satellite tactic differs from the typical “mate guarding” scenario, and instead involves the use of female mimicry to gain access to spawning females (Neff et al. 2002). The bluegill sunfish, *Lepomis macrochirus*, displays similar competition in fertilizing female eggs, with each tactic having different levels of success at fertilizing eggs (Neff et al. 2002).

Social context plays a large role in determining

the sexual behavior of males such as the cactus bug, *Namia femorata*, which creates nests on certain types of cacti, which males use to attract females to lay their eggs. Competition for the nests among males differed depending if the female was present. Male size and hind leg dimorphism was significantly more important when a female was present when competing for a nest (Procter et al. 2012). The domestic canary, *Serinus canaria*, adapts its courting behavior according to who is watching (and their behavior) (Ung et al. 2011). In the cichlid fish, *Astatotilapia burtoni*, subordinate males exhibit a similar alteration of their behavior if seen by dominant males, suggesting they are very much aware of their social environment and alter their behavior accordingly in order to bring about a reproductive advantage (Desjardins et al. 2012).

In the wolf spider *Rabidosa punctulata*, males display different mating tactics. One tactic is normal courtship, including seismic and visual displays. The second tactic is a direct mount; whereby the male ignores courting the female and directly grabs and grapples with the female in an attempt to copulate (Wilgers et al. 2009). This second option can provide a much greater risk for the males when attempting to successfully copulate, as females are generally larger and cannibalistic in nature (Walker; Wilgers et al. 2009). The expression of these alternative tactics have been found to be dependent on both male condition (Wilgers et al. 2009) and mating context, such as predator proximity (Wilgers et al. 2014).

Another context that may influence mating tactic expression in *R. punctulata* is the presence of competing males. In its natural environment, the

number of wolf spiders is quite dense, especially at night in overgrown fields (pers. observation). This is important in context of the experiment, as there are likely multiple males in close proximity all competing for a female. In this situation, the mating tactic that reduces the opportunity for competing males to steal a detected female may bring about a higher chance of reproductive success. Here, we test whether the presence of competing males in the environment affects the mating tactic expression in the wolf spider *R. punctulata*.

MATERIALS AND METHODS

Housing and Rearing: A total of 300 *Rabidosa punctulata*, were collected for the experiment. Spiders were collected on 23-24 August, 2014 from Lincoln, Nebraska. All individual spiders were collected as immatures. The spiderlings were placed in separate, plastic cubic containers, with a cotton wick through the bottom which provided the spiders with water and were fed 2-3 crickets per week.

Data Collection: In order to test whether the presence of a courting male influences another males' mating tactic expression, we exposed males to one of two treatments: 1) Experimental, where a competing male could be detected in the arena, or 2) Control, where no other male was able to be detected. Two arenas were used per trial, one arena for each treatment. Both arenas are identical, with a divider inside in order to keep the competing males separated.

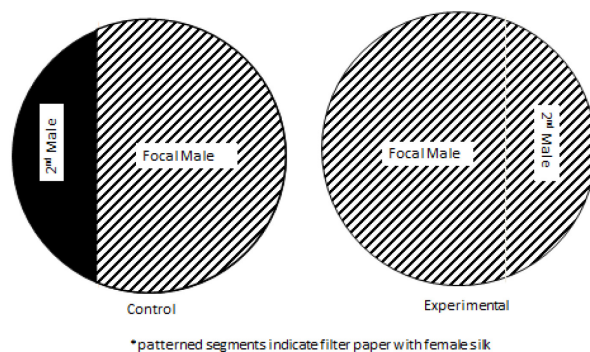


Figure 1. Experimental arenas used to investigate the effects of the presence of competing males on the mating tactic expression in *Rabidosa punctulata*.

Females were placed in separate containers to allow them to lay silk onto filter paper, for at least one hour before the experiment began. Each arena contained a female with a focal male that was allowed to interact with her, and a secondary male that was separated from the focal male and female. Arenas were placed on top of a piece of granite, with

the silk-laden filter paper in between. The Control had the filter paper cut away from the secondary male, while the Experimental did not. The divider on the Experimental arena was modified so as to allow enough space for seismic courtship displays to be sensed across the divider (Figure 1). This setup allowed males in the experimental group to detect the secondary male via seismic cues, while males in the control group could not detect a second male present.

No more than two hours prior to running the trials, the spiders to be used were separately weighed and their mass was recorded. The secondary males were placed into the arenas and once the experimental secondary male began courting, the focal male and female for both treatments were placed into their respective arenas, the time was recorded and data collection began. Once begun, trials lasted 30 minutes, or until copulation occurred. If copulation occurred, the arena/trial that it occurred in was done, but the other arena continued until the end of the time or copulation occurred. The following behaviors were recorded for every trial: tactic used by the focal male, latency to each tactic, # of courtship bouts of the focal male and secondary male (only in the competing male treatment), attacks by the female, copulation, and latency to copulation. 18 trials were conducted and recorded for this study.

Data Analysis: Comparisons were made between the Control and Exposed group using chi-square tests for the following variables: mating tactic, 1st tactic used, copulation success, and tactic used to successfully copulate. We used non-parametric Wilcoxon 2-sample tests to compare the control and experimental groups for the following variables: Female Age & Weight, Focal Male Age & Weight, Courtship Latency, number of Courts, and Copulation Latency.

RESULTS

In total, 36 trials were ran ($N = 18$ / treatment). The focal males used in our experiment were similar across both of the treatment groups in age (Control: $\bar{x} = 36.33 \pm 1.52$; Exposed: $\bar{x} = 36.00 \pm 1.68$; Wilcoxon 2-sample test, $Z = 0.64$, $P = 0.52$) and weight (Control: $\bar{x} = 0.127 \pm 0.0072$; Exposed: $\bar{x} = 0.119 \pm 0.0048$; Wilcoxon 2-sample test, $Z = 0.32$, $P = 0.75$). The females were also similar across both of the treatment groups in age (Control: $\bar{x} = 33.11 \pm 1.54$; Exposed: $\bar{x} = 32.83 \pm 1.63$; Wilcoxon 2-sample test, $Z = 0.19$, $P = 0.85$) but not weight (Control: $\bar{x} = 0.223 \pm 0.0071$; Exposed: $\bar{x} = 0.200 \pm 0.0079$; 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 our focal males, the frequencies of mating tactics witnessed were similar across our two treatments (Figure 2;

Likelihood ratio, $\chi^2_3 = 0.38$, $P = 0.94$).

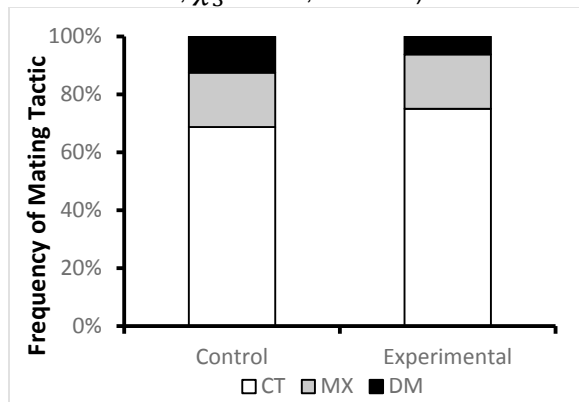


Figure 2. The mating tactic expression of male *Rabidosia punctulata* in response to the presence/absence of a competing male.

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, $\chi^2_1 = 0$, $P = 1.0$). Courtship latency by the focal males were similar across both treatments, no significant differences were found in regards to when courtship began between either treatments (Control: $\bar{x} = 306 \pm 72.22$; Exposed: $\bar{x} = 519 \pm 124.6$; Wilcoxon 2-sample test, $Z = 1.00$, $P = 0.32$). The frequencies of the number of courtships used by the focal males were similar across both treatments as well, introduction of a competing male did not affect the number of times the focal males courted (Control: $\bar{x} = 21.64 \pm 3.97$; Exposed: $\bar{x} = 23.53 \pm 15.11$; Wilcoxon 2-sample test, $Z = 0.24$, $P = 0.81$).

The focal male copulation success was similar across both treatments, exposing a courting male in the environment did not affect the rate of success across either treatments (Likelihood ratio, $\chi^2_1 = 0.45$, $P = 0.50$). Exposure of a courting male in the environment did not affect the copulation latency of the focal males (Control: $\bar{x} = 797 \pm 167$; Exposed: $\bar{x} = 980 \pm 149$; Wilcoxon 2-sample test, $Z = 0.99$, $P = 0.32$). The tactic used when copulation was successful by the focal male was similar across both treatments (Likelihood ratio, $\chi^2_1 = 0.05$, $P = 0.82$).

Variation in secondary male courtship effort did not affect the mating tactic expression of the focal males in the experimental group, as no relationship was detected (Logistic regression; $\chi^2_3 = 2.10$, $P = 0.55$).

DISCUSSION

The results show that no significant differences were found between the control and experimental groups in any way. Through this data we can determine that

for *Rabidosia punctulata*, presence of a competing male in their environment has no influence on the mating behavior used to acquire a mate.

These results were unexpected. Because of the predatory risk involved in the direct mount tactic, it would only make sense for the male wolf spider to use such a tactic when it brings about a fitness advantage over the courtship mating tactic. When presented with a competing male, the focal male would want to use whatever tactic necessary in order to guarantee copulation. However, according to the results, the fitness benefits may not be worth the risk of predation to females. In order to test this, one must analyze the true effect on fitness, which should investigate the direct fitness consequences of mating tactic expression when two or more males are actually competing for access to a female.

While these results were unexpected, new observations have shed some light on these results. A recent study showed that female wolf spiders are actually polygamous, not monogamous (D. Wilgers, personal communication). Through these results it gives light to the fact that the mating behavior of male wolf spiders do not change, since they do not have to necessarily be the first and only mate for the female, they do not have to spend all their energy on being the first to copulate.

Through a wide taxa of organisms, male-male competition brings about alternative mating tactics which are used to maximize reproductive fitness, which widely vary depending on the risks involved and the given social environment. While some alternative tactics bring about an additional risk to predation, they often become worthwhile as long as fitness is increased. This study has shown that in the male wolf spider, *Rabidosia punctulata*, the direct mount tactic is not preferred in situations where a competing male may hinder another's chance at copulation. While previous evidence suggests that it should, new information provides a reasonable and obvious explanation for such an exception: that the female wolf spider can accept more than one mate at a time. This study supports that realization, and gives new information on this species of wolf spider that was previously unknown.

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