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SHORT COMMUNICATION

Field observations of simultaneous double mating in the wolf spider *Rabidosa punctulata* (Araneae: Lycosidae)

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Abstract. Males of many species of spider engage in alternative mating tactics that do not involve pre-mating courtship. Here I report field observations of a novel opportunistic mating tactic of the wolf spider *Rabidosa punctulata* (Hentz, 1844): simultaneous double mating, whereby males that encounter copulating pairs also mount and achieve inseminations concurrently with the first male. On three separate occasions, female *R. punctulata* were observed mating with two males simultaneously. Males that mate with already copulating females likely receive multiple fitness benefits. It may allow courtship parasitism of other males while also reducing male agonistic interactions, eliminate the need to court or subdue the female, and reduce pre-mating cannibalism risk. If such behavior is common, it may limit sexual selection acting on male courtship displays by reducing the effectiveness of pre-mating female choice while also increasing sperm competition.

Keywords: Polygynandry, lycosid, threesome, satellite male, sperm competition

Males of many species of spider engage in alternative or opportunistic reproductive tactics to maximize fitness under different conditions (reviewed in Robinson & Robinson 1980; Christenson 1984). Males may engage in sneak copulations (Elgar & Fahey 1996; Schneider et al. 2005), mate with recently molted (Jackson 1986) or feeding females (Prenter et al. 1994; Elgar & Fahey 1996; Fromhage & Schneider 2005) or even mate with immature spiders (Biaggio et al. 2016). These behaviors may have evolved to minimize female mate choice or reduce the risk of pre-mating sexual cannibalism. Other strategies like coercive or direct mounting of females in the absence of courtship may have evolved in response to competition from rival males in the area as well as to override female mate choice (Johns et al. 2009; Wilgers et al. 2009; De Young & Wilgers 2016). Females may choose males using a courtship threshold rule whereby they accept any male that exceeds a specified level of courtship. If females use a courtship threshold rule for choosing males and don't discriminate the source of the courtship, non-courting males may be able to successfully parasitize the courtship displays of accepted males by mounting the female while another male courts. This pattern has been documented in the Australian redback spider (*Latrodectus hasselti* Thorell, 1870) (Stoltz & Andrade 2010). Among these examples of opportunistic mating strategies, males are able to successfully mate without courting. Male spiders may be able to adaptively combine strategies that minimize cannibalism with strategies that minimize courtship by approaching distracted females already copulating with a male, directly mount the female, and achieve inseminations concurrently with the first male. Although this behavior is possible given the paired structure of male and female genitalia, it has been poorly documented in the spider literature. Here I describe natural occurrences of this behavior in a single species and also discuss the possible adaptive advantages to males.

In the fall of 2015, three separate observations of two male *Rabidosa punctulata* (Hentz, 1844) (Araneae: Lycosidae) simultaneously mating with a single female were found under natural field conditions. All observations occurred within a three week time frame between October 3rd and October 24th. Spiders were serendipitously discovered while hand-collecting other species of wolf spider by headlamp. All three mating triads were observed between 1850 and 2300h and occurred on short lawn grass in the front yard of my house in Selinsgrove, Snyder County, Pennsylvania, USA. During the first two observed simultaneous double matings, both males were discovered already mounted on the female. Mounting time lasted for 43 minutes and 61 minutes respectively for these mating triads between the time of discovery until one of the males dismounted. In both mating triads, males shifted positions until they were each able to access at least one spermatheca. Although simultaneous insertions from different males were not directly observed in either of the first two triads, alternating leg spine erection among both males was observed in very close succession and over several minutes suggesting that alternating hematodochal expansion was occurring for each male. This pattern was verified in the third triad observation.

During the initial observation of the third triad, I was able to observe a courting male begin mounting a female within a few minutes while a second male was approaching the same female within a few centimeters away. The second male did not court and also mounted the female within one minute of the first male's mount. I then left for about four minutes to retrieve my camera and a plastic lid from my house and returned to the mating spiders. I noted the time again and positioned the plastic lid under the mating triad and transported all three to my dining room table for photographing (see Figs. 1A–E). Neither male dismounted the female during transport nor did they shift position. I then placed the triad inside a large plastic sweater box (59.7 cm x 47.9 cm x 14.9 cm) for continuous observations and macrophotography. None of the three spiders were touched nor were they contacted except with placement of the lid under the triad. All photos were the result of 3–6 focus-stacked images using Zerene® Stacker software. This allowed increased depth of field and better documentation of leg positions and pedipalps for both males. Photos were taken using a Canon® 6D and MPE-65mm 1-5x macro lens with a Canon® MT-24EX macro twin lite flash mounted to the lens. I was able to individually identify the males because the second mounted male (B) had one leg II missing. Mounting time of both males persisted for at least four hours. The first male (A) mounted the female at approximately 1901h with the second male (B) initiating a mount less than one minute later. Both males were still mounted four hours later at 2301h when direct observation ceased. I returned at 0500h the following morning to find both males dismounted and no cannibalism evident. An additional leg was missing from male B however, suggesting some aggression. All three spiders were returned to the field that morning.

In all three mating triads, the spiders spent most of the observation time in one of three positions with the remainder of the time

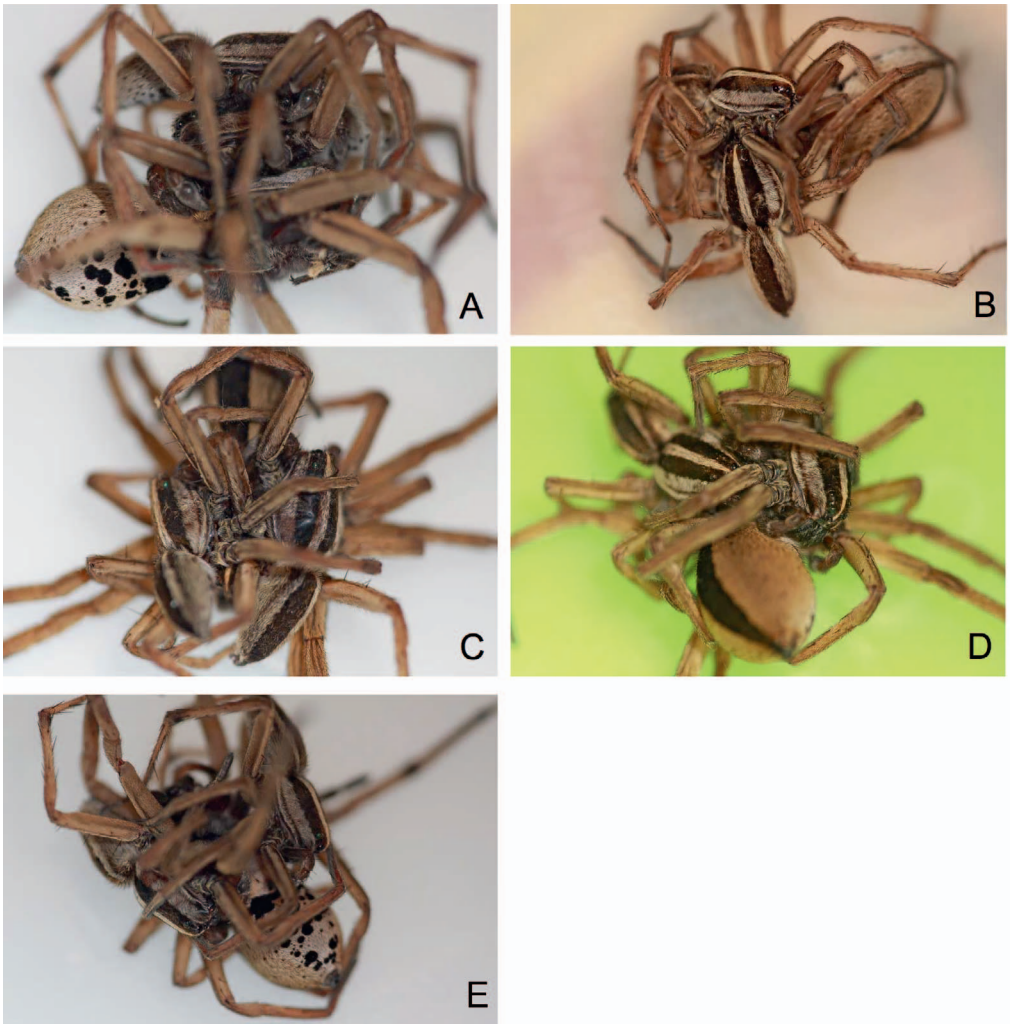

Figure 1.—Simultaneous double mating in the wolf spider *Rabidosa punctulata* (Lycosidae). A. Position one with the second male mounted dorsally on the first male in an anterior-to-posterior direction. The top male scraped his pedipalp along the lateral side of the second male's abdomen, presumably in a failed attempt to locate the epigynum (9.6% of total copulation time). B. Position two with one male oriented at 90 degrees relative to the other male. Both males are in a ventral-ventral position relative to the female with the female inverted on her dorsum (12.1% of total copulation time). C–E. Position three with both males in an anterior-posterior position relative to the female but displaced laterally (75.4% of total copulation time). C. Dorsal view with both males' legs intertwined to maintain position. D. Female rotating abdomen to accommodate one of the male's pedipalps. E. Ventral view with one of the male's pedipalps nearly inserted while the other male waits for the female to rotate her abdomen the other direction for his turn at insertion.

transitioning between these positions. The percentage of time mounted in each of these positions was documented only for the third mating triad and is described below.

For position one, one male is mounted dorsally but in an anterior-to-posterior direction with respect to the other male, which in turn, is mounted anterior-to-posterior dorsally on the female (Fig. 1A). While in this position, the dorsal-most male exhibited palpal moistening and palpal scraping along the antero-lateral portion of the lower male's abdomen, apparently trying to locate the epigynum (Fig. 1A). At the same time, the male immediately dorsal to the female was able to engage in palpal insertions. This orientation occurred with both males at various times occupying the lower position closer to the female. This position comprised only 23 minutes (9.6%) of the total observed mounting time.

Position two was observed with each male oriented at a 90 degree angle from one another in a ventral-ventral position relative to the female. In this position, the female was inverted on her dorsum (Fig. 1B) and the male oriented closest to the long axis of the female was able to achieve insertions. The other male oriented at 90 degrees was unable to gain an insertion but did interfere with the first male's insertion with repeated palpal scraping at the other male's palps. This resulted in several partial hematodochal expansions of the first male's palp outside of the female's reproductive tract. It was unclear if these pedipalp sparrings were the incidental by-product of one male's failed insertion attempts or a direct attempt at copulatory interference. This position accounted for 29 minutes of the observed mounting time (12.1%).

The third position made up the majority of the observation period (181 minutes or 75.4% of mounting time) with the remaining seven minutes (2.9% of mounting time) consisting of males in transition between one of these three positions. Position three consisted of both males in an anterior-to-posterior position dorsally on the female and resembled a typical Type III mating position for lycosids (Foelix 1996) with the exception that both males were somewhat displaced laterally (Figs. 1C–D). While in this position, both males were able to successfully insert pedipalps into the female alternately as the female

rotated her abdomen to one side or the other but only with one of their pedipalps. This frequently required both males to move to a lateral position on the female to accommodate an insertion (Fig. 1E, ventral view). While in the third position, the males never switched sides of the female during the entire observation period. No overt aggression was witnessed during the entire four-hour observation period.

Prior to these observations, I had never seen even single copulating pairs of *R. punctulata* in the field. It was therefore surprising that three observations occurred within a short period and all of them involved mating triads of *R. punctulata*. This suggests that simultaneous matings of *R. punctulata* may be particularly common in the field for at least this population of the species. Although spider densities were not exhaustively sampled, over twenty individuals occurred over a 6 m^2 area within the yard when the third mating triad was observed. Minimum density estimates were not noted for the first two triad observations but all three mating triads occurred within 21 days of each other and in the same general area so presumably had similar population densities. It is possible that these events are the result of unusually high *R. punctulata* densities and therefore illustrate an atypical behavior. A recent laboratory study with experimental triads of two male *R. punctulata* paired with a single unmated female failed to result in simultaneous matings (De Young & Wilgers 2016) suggesting that either laboratory matings may underestimate the occurrence of this behavior or that different environmental conditions are necessary to promote this particular alternative mating strategy. De Young & Wilgers (2016) found that males tended to be successful with a direct mount rather than courtship strategy when two males were interacting with a single female and both males showed some mating behavior. Mountings of the first male were disrupted in 50% of cases by the second male but no simultaneous matings were reported where both males remained on the female.

There are several potential adaptive advantages to mounting an already-mating female compared to mating first, or waiting until a male dismounts and then attempting to mount. First, courtship may be unnecessary when approaching a copulating female (Wilgers et al. 2009). Since many wolf spider courtship displays can attract predators (Pruden & Uetz 2004; Hoefler et al. 2008; Roberts & Uetz 2008; Fowler-Finn & Hebets 2011a, b; Wilgers et al. 2014; Clark et al. 2016) males may minimize their own predation risk while another male courts. If female *R. punctulata* don't discriminate the source of the courtship as in the Australian redback spider and females follow a threshold courtship rule for mating (Stoltz & Andrade 2010), then the opportunity cost of choosing to not court a female may be small. Second, wolf spider courtship is energetically expensive to males (Kotiaho et al. 1998; Hoefler et al. 2008; Cady et al. 2011) allowing courtship parasitizing males to conserve energy for copulation itself or for seeking additional females. Third, males that wait until a pair are mating may suffer reduced pre-mating cannibalism compared to males that are first to initiate courtship or choose to mate with recently mated females. Mating females may be distracted, catalyptic, or immobilized by the male. In this way, copulating females may be functionally equivalent to a feeding or recently molted female that shows little or no aggression toward males (Jackson 1986; Prenter et al. 1994; Fromhage & Schneider 2005). In some cases, mating males may actually induce a quiescent state in the female, making cannibalism less likely (Becker et al. 2005). Previous studies show that mated female wolf spiders exhibit significantly higher pre-mating cannibalism frequencies than unmated females (Persons & Uetz 2005) indicating that if secondary males wait until the first male dismounts, sexual cannibalism risk will increase. A fourth related benefit includes reduced risk of being rejected by an already mated female. For some wolf spider species, females tend toward monandry and have low frequencies of second matings even if they don't cannibalize (Norton & Uetz 2005; Persons & Uetz 2005; Jiao et al. 2011). A fifth benefit of simultaneous mounting may include a reduced chance of direct agonistic interaction between males since non-mating male wolf spiders may spar and grapple with each other, especially in the presence of an unmated female (Aspey 1977a, b; Delaney et al. 2007; Hoefler et al. 2009). Finally, male mounting of copulating females may eliminate the need for aggressive tactics toward the female which may injure both the female and potentially result in the death of the male (Johns et al. 2009; Wilgers et al. 2009)

Despite these adaptive benefits of simultaneous mating, there are several apparent costs. Male-male interference that could reduce sperm transfer and increase the energetic costs of mating are likely. In my direct observations, males showed palpal sparring, missed insertions, attempts at pedipalp insertions into the other male's venter, and attempts to displace the other male during insemination. Collectively, these inefficiencies may lead to prolonged matings. Longer copulation is associated with increased risk of post-mating cannibalism among some wolf spiders (Wilder & Rypstra 2007) and may make spiders more susceptible to other predators. Stratton et al. (1996) reported maximum copulation durations for *Rabidosa hentzi* (Banks, 1904) and *Rabidosa rabida* (Walckenaer, 1837) at 25.67 minutes and 90 minutes respectively. Our minimum copulation duration of four hours for one of the observed triads suggests that simultaneous matings extend copulation duration. For many lycosids, prolonged copulation may serve as a form of mate guarding to reduce sperm competition while the sperm capacitates (Stratton et al. 1996; Szirányi et al. 2005). Such mate-guarding functions of prolonged mating would be ineffective under conditions of simultaneous mating. In *R. punctulata*, direct mounting without courtship is condition-dependent, with larger, better condition males adopting this strategy more frequently than small poor-condition males (Wilgers et al. 2009). My observations suggest that non-coercive direct mounting of copulating females may make direct mounts far less risky for poor-condition males.

Collectively these observations have important implications for our understanding of the strength of intersexual selection acting on male courtship displays, the nature of male-male competitive interactions before and during mating, sperm competition, and cryptic female mate choice. These observations also expand on the diverse repertoire of opportunistic mating tactics exhibited by male spiders. Most intriguing, secondary mounting strategies can result in male mating success without courtship, female acceptance, or overt coercive behaviors toward females, all while reducing pre-mating cannibalism risk. If so, then males that are at a competitive disadvantage through either courtship or aggressive mating tactics may engage in this strategy to achieve some fitness benefits. Although not directly observed here, courtship parasitism of attractive males or parasitism of other male subjugation of females may be a viable strategy for improved mating success for less competitive males. Additional research on the taxonomic occurrence, frequency, and social context of this behavior is needed.

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