2008. The Journal of Arachnology 36:533–537

# Frequency and consequences of damage to male copulatory organs in a widow spider

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**Abstract.** Copulatory organ breakage, in which a portion of the male's genitalia breaks off and remains in or attached to the female's genitalia may represent a male strategy of high investment in a single mating. Such a strategy is expected when mating opportunities for males are limited and competition for females is high. We studied costs and benefits for males as a consequence of male organ breakage in the white widow spider (*Latrodectus pallidus* O. Pickard-Cambridge 1872). In order to estimate the frequency and consequences of such damage we provided each male with four virgin females simultaneously in an outdoors enclosure. We recorded male mating success and loss of the tip of the embolus (the male intromittent organ) inside the female's genitalia for each male. In order to test the effect of the broken tip as a mating plug, we collected females from natural populations and observed the location of embolus tips inside their genitalia. We found that damage to the male organ was frequent but did not necessarily result in male sterility. From the field data, we found that the likelihood of a second embolus tip entering the spermatheca is significantly lower than that of the first tip, suggesting the possibility that the tip functions as a partial mating plug.

**Keywords:** Male mating strategy, embolus tip, *Latrodectus pallidus*

The reproductive success of a male is usually a function of the number of females he inseminates, especially when males produce numerous gametes and when little time and energy is spent on care of offspring. Under these circumstances each male is expected to mate with many females (Darwin 1871; Bateman 1948; Trivers 1972; Andersson 1994). Nevertheless, in some cases males invest highly in a single female. This investment may increase the male's reproductive success in the current mating but dramatically reduce the number of matings that he can potentially achieve. Such a strategy can be promoted by evolutionary processes if the probability of encountering and mating with an additional receptive female is sufficiently low (Parker 1979; Buskirk et al.1984; Elgar 1992; Simmons et al. 1992; Parker 1998; Andrade 2003) and if males strongly compete for females (Thornhill 1980; Fromhage et al. 2005).

Copulatory organ breakage, in which a portion of the male's genitalia breaks off during copulation is relatively common in spiders (Wiehle 1967; Breene & Sweet 1985; Foelix 1996; Schneider et al. 2001; Miller 2007). Broken organs inside the female's genitalia may function as a mating plug to prevent fertilization by later arriving males, but it may also reduce the probability of the male fertilizing additional females (Foelix 1996). Thus, this trait may represent a male strategy of high investment in a single mating. To date, few studies have quantified the costs and benefits of male organ breakage. In the spider *Nephila funestrata* Thorell 1859, for example, males often damage both of their paired mating organs while copulating with a single virgin female (Fromhage & Schneider 2005). The occurrence of a male organ part inside the female's genitalia was shown to reduce the number of copulatory insertions by a second male (Fromhage & Schneider 2006). Similarly, in *Argiope bruennichi* Scopoli 1772, males can use each copulatory organ once, and insertions into a previously used insemination duct were significantly shorter when the previous male had left parts of his genitalia inside the insemination duct (Nessler et al. 2007).

In widow spiders (*Latrodectus*), the tip of one or both of the male's intromittent organs (emboli) often breaks-off during copulation to be left inside the female's genitalia (Levi 1959; Bhatnagar & Rempel 1962; Wiehle 1967; Kaston 1970; Berendonck & Greven 2002; Segoli et al. 2006). Males without embolus tips were assumed to be functionally sterile (Bhatnagar & Rempel 1962; Foelix 1996), but there is evidence that this is not always the case, as shown in *L. mactans* Fabricius 1775 (Breene & Sweet 1985) and *L. hasselti* Thorell 1870 (Snow et al. 2006). It was suggested that a tip inside the female's spermatheca functions as a mating plug (Foelix 1996; Berendonck & Greven 2002); however, this was demonstrated only in *L. hasselti*. In this species first male sperm precedence was found when two males inseminated a single genital pore (Snow & Andrade 2005) and when the first tip was deposited in the entrance of the spermatheca (Snow et al. 2006). In several other *Latrodectus* species, however, more than one tip can be found inside the female's spermathecae (Uhl 2002), suggesting that the embolus tip is not totally effective as a mating plug.

In this study we investigated two aspects of the adaptive value and costs of damage to the male organ in the white widow spider, *Latrodectus pallidus* O. Pickard-Cambridge 1872: 1) future inseminating opportunities for males who have broken emboli (male sterility hypothesis) and 2) the risk of sperm competition (mating plug hypothesis). Males of this species suffer high extrinsic mortality and normally do not encounter more than one female in natural conditions, while females are often polyandrous (Segoli et al. 2006). Thus, males that encounter a virgin female would benefit from blocking the spermatheca of their mate and thereby reducing or preventing access to future rivals. There is evidence that *L. pallidus* males invest highly in each mating: they cohabit in females' webs longer than required for mating (Segoli et al. 2006), engage in an energetically demanding courtship display (M.S. personal observations), and are sometimes cannibalized by the female (Segoli et al. 2006). Thus, breakage of the male organ may be an integral part of the male mating strategy in this species even at the cost of a limited fertilization success in the future.

In order to estimate the frequency and consequences of male organ breakage we asked the following questions: 1) How frequently do embolus tips break? 2) Does the loss of embolus tips prevent the male from remating? and 3) does the presence of a tip inside the female's spermatheca reduce the probability of another tip entering the spermatheca? In order to answer the first two questions we conducted an experiment in which we provided 21 males each with four virgin females simultaneously in outdoor enclosures. Thus, each male had the opportunity to possibly mate with four females. For each male, we recorded fertilization success and the loss of embolus tips by recording the successful production of viable egg sacs in females and by recording the presence of the embolus tips in the genitalia of the females. In order to answer the third question, we collected females from natural populations and recorded the location of male tips inside their genitalia.

## METHODS

The white widow spider (*L. pallidus*) is common in the Negev desert of Israel (Levy 1998). We collected males and females from the Sede Teman area (31°17′N, 34°43′E) and Sayeret Shaked Park (31°16′N, 34°38′E) (northern Negev, Israel) in April 2003. Voucher specimens were deposited in the National Collection of Arachnids, Hebrew University of Jerusalem. Spiders were collected as juveniles or sub-adults and reared to maturity under lab conditions on the Sede Boqer Campus of Ben-Gurion University. Males were kept in plastic cups (200 cc) and fed weekly with *Drosophila*. Females were kept in terraria (10 × 20 × 15 cm) containing small dry shrubs, on which they constructed their webs. Females were fed weekly with flour beetles (larvae of *Tenebrio molitor*), crickets (*Acheta domestica*), grasshoppers (*Schistocerca* sp.) and houseflies (*Musca domestica*).

**Enclosure experiment.**—We placed four adult virgin females with their webs in a square outdoor arena (135 cm length × 135 cm width × 50 cm height), one in each corner. Each arena was constructed from a wooden base and frame with plastic sheets as walls and a removable mesh cover. Females were not fed during the trial. Once the females repaired their webs (~1 day), we placed one adult naïve male in the center of each arena ($n = 21$ replicates). The location and activity of the male (no movement, courting, in mating position) were recorded three times a day until it died. The number of daily observations was determined from preliminary observations, which indicated that males stay at least one day with each female. Females were measured and weighed at the end of each trial. They were kept until they produced seven egg sacs or until two months passed without laying eggs. Females that produced fertile egg sacs were assumed to have mated. This assumption is valid because mated females kept with adequate food rarely fail to produce fertile egg sacs (M.S. personal observations). The reproductive success of females was measured by the total number of eggs and by the number of fertile eggs (eggs that hatched) from the first five egg sacs. We used data from the first five egg sacs since most females lay 1–3 egg sacs in the field and five egg sacs was the maximum observed in nature (M.S. personal observations). Post mortem we checked females' spermathecae for the presence of embolus tips. Females have paired copulatory ducts, each leading to a spermatheca, and males have paired intromittent organs (emboli). During mating, the male inserts one embolus at a time into one of the female's genital openings. Thus, a male may leave none, one, or both tips (one in each side) in the genitalia of a female. We obtained complete data on male embolus tips in the genital tracts of all four females from 15 trials. Spermathecae were examined by placing them in a 5% KOH solution; after a week the tissue became transparent and the embolus tips were visible under a dissecting microscope (Berendonck & Greven 2002). For each trial we determined the order and number of females the male visited, which of the females he inseminated, the reproductive success of each female and finally, which females possessed embolus tips inside the spermathecae.

**Females collected from the field.**—We collected 216 adult females from their webs at three locations in Israel: Goral Hills, near Lehavim (31°22′N, 34°49′E, $n = 192$), Kfar Edomim (31°49′N, 35°19′E, $n = 13$), and Sayeret Shaked (31°16′N, 34°38′E, $n = 11$) from March 1998 till September 1999. Egg sacs, if present, were left unharmed in the web. We dissected the females, removed their spermathecae and copulatory ducts, placed them in a 5% KOH solution and examined them for the presence of embolus tips as above. Since the number of tips in the right and left genitalia were correlated (Spearman rank correlation, $n = 216$, $R_s = 0.632$, $P < 0.01$), we considered only the right spermatheca and copulatory duct of each female, thereby avoiding pseudoreplication.

We compared cases in which one male tip was found in the female genitalia (genital duct + spermatheca) to cases in which two tips were found. We estimated the probability of a first embolus tip to enter the spermatheca as the percentage of females with an embolus tip located inside the spermatheca out of the total number of females with one embolus tip found in their right genitalia. We compared this with the probability of a second tip entering the spermatheca: the percentage of females with two tips inside the spermatheca, out of the total number of females with two tips in their right genitalia. We expected that if the first tip prevents the second tip from entering the spermatheca, the probability of finding a second tip inside the spermatheca would be lower than for the first tip.

## RESULTS

**Enclosure experiment.**—After placement in the arena with the four females, males started courting one of the females. Courtship included the following behaviors: adding silk to the female's threads, vibrating the web and cutting sections from the web. Mating was difficult to observe since it took place inside the female's retreat. On the following days males were observed courting or standing motionless on the web, either inside or outside the retreat. The median time from the

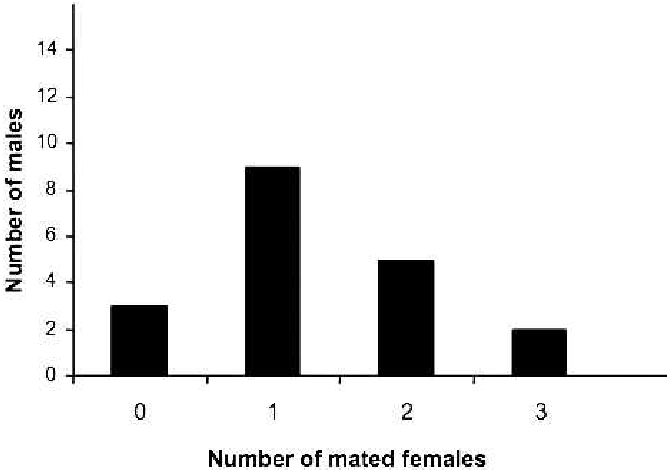

Figure 1.—Number of males that mated with 0–3 females ($n = 19$ trials). Each male was provided with four virgin females simultaneously in an outside enclosure.

introduction of the male into the arena with females until the death of the male was 5 days (range 1–23 days, $n = 21$). One male escaped from his arena and entered another arena. He was returned to his arena after visiting one female in the adjacent arena. We excluded the two males from these two arenas from analyses of the number of mated females.

Three males out of 19 did not inseminate any female, most of the males inseminated one or two females and two males inseminated three females (Fig. 1). The proportion of inseminated females was higher among females that were visited first (77%) than among females visited later (41%) (Fisher's exact test, $n = 22$ for first females and $n = 29$ for females visited later, $P = 0.02$).

Three mated females died during the experiment and the remaining mated females produced seven egg sacs before the end of the experiment. The mean number of eggs per egg sac was 130 ± 30 (± SD, $n = 30$ females; averages of eggs per sac for each female were averaged over all females) and the number of hatched eggs was 103 ± 40. The total number of eggs that were produced by mated females in the first five sacs was not influenced by the number of embolus tips inside their spermathecae nor by mass, size, or age of females (GLM stepwise backward model, $n = 25$, $P > 0.1$ for all). The results were still not significant when considering hatched eggs only. Thus, there were no differences among the females in their reproductive success.

Six out of 21 males (29%) were cannibalized by females. Cannibalism was observed directly or could be inferred from the transparent body of the dead male found on the female's web. In five out of six cases the cannibalistic female did not produce egg sacs, indicating that cannibalism occurred before copulation, or that the female did not use the male's sperm for fertilization.

Data on the presence of male embolus tips in the genitalia of females and fertilization success are presented in Table 1. Three males did not lose any embolus tip with the first female they visited; nevertheless, one of these fertilized the female. Four males lost one embolus tip in the first mating. Two of these fertilized the first female only and the other two fertilized one and two additional females. Eight males lost both embolus tips in the first mating. Four of these fertilized the first female only, three fertilized an additional female, and one fertilized two additional females.

Table 1.—Embolus tips inside spermathecae and fertilization of 1st, 2nd, and 3rd females visited by 15 males in the arena experiment. Numbers in columns represent the number of tips found in the female spermathecae. Shaded cells indicate that the female produced fertile egg sacs.

| # males | First | Second | Third |
|---|---|---|---|
| 2 | 0 | 0 | 0 |
| 1 | 0 | 0 | 0 |
| 2 | 1 | 0 | 0 |
| 4 | 2 | 0 | 0 |
| 3 | 2 | 0 | 0 |
| 1 | 2 | 0 | 0 |
| 1 | 1 | 1 | 0 |
| 1 | 1 | 1 | 0 |

**Females collected from the field.**—Forty-eight out of 216 females contained no embolus tip inside their right genitalia. In 86 cases out of the 95 females that contained one tip in their genitalia, the tip was placed inside the spermatheca, and in nine cases the tip was located in the genital duct. Thus, we estimated the probability for the first tip in the female's genitalia to enter the spermatheca as 0.9. We found 58 females with two embolus tips inside their right genitalia. Out of these, in three cases both tips were located in the genital duct, in 28 the two tips were placed inside the spermatheca, and in 27 one tip was placed inside the spermatheca and the second was in the genital duct. Thus, we estimated the probability of a second tip to enter the spermatheca as 0.5. The likelihood of a first tip to enter the spermatheca was significantly greater than the likelihood of a second tip to enter the spermatheca (Fig. 2, Fisher's exact test, $P < 0.0001$). Additionally, fourteen females contained three tips in their right genitalia. Of these, one female had no tips inside the right spermatheca, 8 had one tip, two had two tips and three had three tips. Finally, one female contained five embolus tips, four of which were found inside the spermatheca.

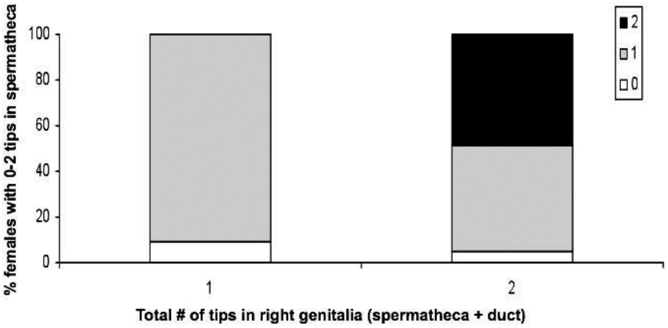

Figure 2.—Embolus tips found in the spermatheca alone and in the entire genitalia: percentage of females with no embolus tips (white section), one embolus tip (gray section) or two embolus tips (black section) inside their right spermatheca, out of field-collected females with either one ($n = 95$) or two tips ($n = 58$) in their right genitalia (spermatheca + genital duct).

## DISCUSSION

In this study we estimated the frequency and consequences of damage to the male copulatory organ in the white widow spider *L. pallidus*. We found that damage to the male organ was frequent but did not necessarily result in male sterility. We showed that the occurrence of a male's embolus tip inside the female's spermatheca functions as a partial mating plug: it probably obstructs but does not always prevent the entrance of an additional tip into the spermatheca.

In contrast to our study, male sterility following damage to the male copulatory organ has been demonstrated in several spider species. For example, in *Argiope keyserlingi* Karsch 1878, experimental removal of one copulatory organ prevented males from copulating with more than one female, suggesting that males can use each of their paired organs only once (Herberstein et al. 2005). In *Nephila funestrata*, 95% of the males mating with a virgin female had a damaged organ that probably prevented them from remating (Fromhage & Schneider 2005). In widow spiders the loss of an embolus tip inside the female genital tract was previously assumed to result in functional sterility of the male (Bhatnagar & Rempel 1962). Breene & Sweet (1985), however, found that some males of a congener (*L. mactans*) were able to successfully inseminate three females suggesting that males either do not always lose their tips or that they can inseminate in spite of embolus breakage. In *L. hasselti*, males are normally sterile after mating (Andrade & Banta 2002), but when tips were cut experimentally males were able to inseminate additional females (Snow et al. 2006). Thus, the loss of embolus tips alone cannot be responsible for the post-mating sterility in *L. hasselti*. In our study we found that at least one male mated and inseminated a female without losing any embolus tip and five males inseminated one or two females after losing both tips in previous matings. Thus, we suggest that the loss of embolus tips in *L. pallidus* is common, but does not prevent the male from fertilizing additional females.

Although damage to the copulatory organ in *L. pallidus* was not an absolute constraint on the male's reproductive success, only a few males (2 out of 19) inseminated more than two females. This suggests that insemination with a broken embolus is mechanically difficult and is less likely to be successful than insemination with an intact embolus. Additionally, in the absence of tips, males may have difficulties filling their emboli with sperm (sperm induction) and therefore low fertilization success may result from sperm depletion rather than an inability to transfer sperm (Snow et al. 2006). However, it is not yet known whether white widow males refill their emboli between mating attempts. Finally, insemination with a broken embolus may be especially difficult when mating with an already mated female with a plugged spermatheca. If so, embolus breakage may still carry a cost for males in mating systems where sperm competition exists.

Although males were not competing for females in this experiment, there is evidence that embolus breakage may give the males an advantage in sperm competition. Most of the males that lost both tips (8 out of 10) left them in each of the two spermathecae of the first female that they mated, indicating that they had mated with her twice. However, there was no difference in the reproductive success of females with one or two tips in their spermathecae. A similar result was obtained in a study of *L. hasselti* where repeated mating did not increase the probability of successful fertilization nor the number of offspring produced in successful matings (Andrade & Banta 2002). We suggest that males leave both tips in order to protect both of the female's spermathecae from future insemination by rival males.

The analysis of spermathecae from females collected in the field further supports the view that the broken embolus functions as a partial mating plug. The probability of a first embolus tip entering the spermathecae was significantly higher (90%) than that of the second tip (50%). It is also possible that a second tip replaced the first, but this is unlikely considering the narrow entrance to the spermatheca (Berendonck & Greven 2002). However, the results also suggest that the tip is not totally effective as a plug: in half of cases a second tip **did** enter the spermatheca, and in four cases more than two tips entered the spermatheca. In contrast, in a study of *L. hasselti* it was shown that in ~90% of the cases where two males inseminated the same genital pore, the second tip did not enter the spermatheca resulting in a first male sperm priority (Snow et al. 2006). Although it is difficult to compare the results of this controlled experiment with our field data, it implies that the plug in *L. hasselti* is more efficient than in *L. pallidus*. From an evolutionary point of view, the differences in the efficiency of the plug between species may reflect an arm-race between males and females over control of paternity. In this light it would be interesting to compare the efficiency of the plug in different *Latrodectus* species in relation to mating opportunities, effective sex ratio, and sexual cannibalism.

In contrast to embolus tip breakage, sexual cannibalism does not seem to be an integral part of the male mating strategy in *L. pallidus*. In *L. hasselti*, males initiate cannibalism by placing their abdomen in front of the female's mouthparts during copulation: cannibalized males copulate longer and cannibalistic females are less likely to remate (Andrade 1996). Similar sacrificial behavior was also observed in *L. geometricus* C.L. Koch 1841 (Segoli et al. 2008). In *L. pallidus*, however, most of the cannibalized males (5 out of 6) did not fertilize the cannibalistic female and thus could not benefit from cannibalism. This illustrates the distinction between male sacrifice behavior as an adaptive strategy and cannibalism as an unavoidable consequence of mating with a dangerous partner.

In conclusion, damage to male copulatory organs is consistent with a male strategy of high investment in a single female. Embolus damage does not necessarily result in male sterility and may provide some paternity advantage over subsequent males. This benefit will be expressed only when females mate multiply and when mating opportunities are limited for males, as is the case in the mating system of white widow spiders (Segoli et al. 2006).

## ACKNOWLEDGMENTS

We thank Iris Musli, Efrat Gavish, Alexei Maklakov, Dinesh Rao, Yael Teleman, Moran Segoli, Tamar Keasar, and Jutta Schneider for discussions and assistance, and two anonymous referees for valuable comments on the manuscript. This is publication no. 613 of the Mitrani Department of Desert Ecology.

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*Manuscript received 13 May 2007, revised 30 April 2008.*