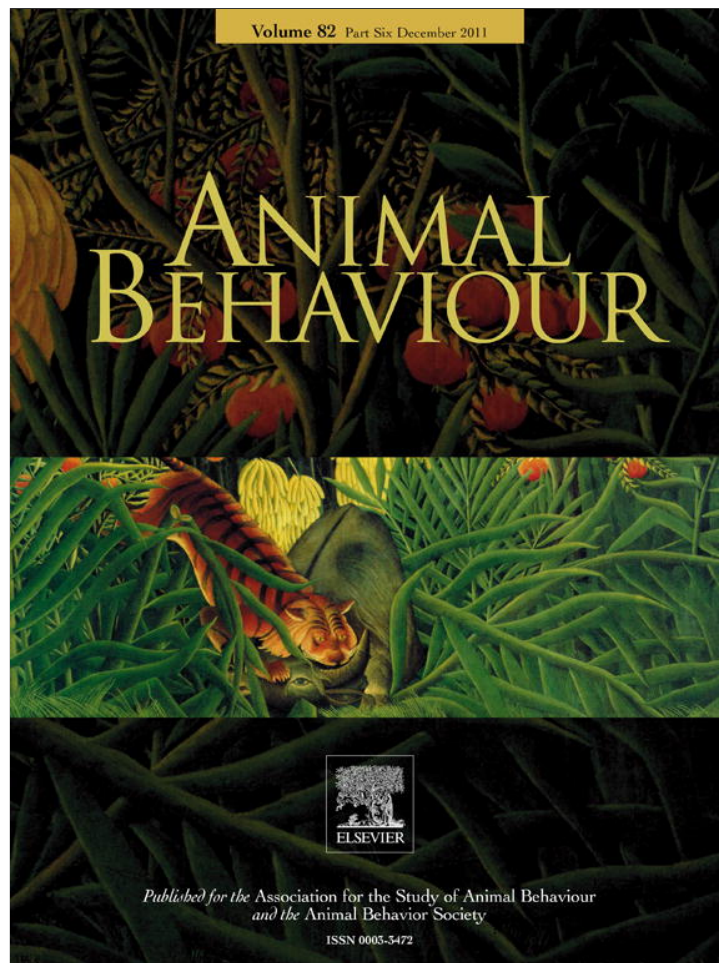


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Mate binding: male adaptation to sexual conflict in the golden orb-web spider (Nephilidae: *Nephila pilipes*)

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To counter female resistance to mating and cannibalism, males of many animal species have evolved a variety of behavioural adaptations. Here we investigated a novel copulatory courtship behaviour, mate binding, in which the male deposits fine silk onto the female's body in between copulation bouts, in an orb-web nephilid spider, *Nephila pilipes*. We hypothesized that mate binding might reduce female aggressiveness and sexual cannibalism and that both tactile and chemical cues play a role. We performed a series of mating trials, in which we blocked (1) the females' tactile perception, (2) the females' chemoreceptors, and (3) both types of communication. We also manipulated male spinnerets and thus male silk production. As predicted, mate binding reduced both female resistance to repeated mating and levels of sexual cannibalism. Our results suggest that both tactile and chemical cues are crucial for mate binding to succeed in rendering females less aggressive, but that tactile cues are more important. We conclude that mate binding prolongs total copulation duration, whereby the male maximizes his paternity. Therefore, mate binding may serve as a mechanism countering sexual conflict over repeated mating and sexual cannibalism.

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Sexual conflict arises when the reproductive interests of the two sexes diverge and is ubiquitous in animals (Parker 1979; Arnqvist & Rowe 2005; Chapman 2006). Male reproductive success largely depends on the number of females the male fertilizes, and males are thus expected to maximize the number of mates. On the other hand, females may seek to mate with only higher-quality males, and are thus expected to be more reluctant to mate or resist mating by males frequently (Andersson 1994). Sexual cannibalism, where an aggressive female attacks, kills or consumes a male during a sexual encounter, may represent the ultimate sexual conflict (Elgar 1992; Elgar & Schneider 2004). Theory predicts that sexual conflict can lead to antagonistic coevolution, in which adaptations in each sex select for counteradaptations in the other (Parker 1979; Arnqvist & Rowe 2005; Chapman 2006; Tregenza et al. 2006). Female resistance to mating/remating and the risk of female cannibalism will promote a variety of male adaptations to

circumvent or mitigate the conflicts over mating and sexual cannibalism. Indeed, a wide variety of behavioural, morphological and physiological male traits have been suggested to reduce female resistance to mating/remating and the risk of female cannibalism (e.g. Lawrence 1992; Johnstone & Keller 2000; Elgar & Schneider 2004; Arnqvist & Rowe 2005; Wedell et al. 2006; Miller 2007; Rönn et al. 2007; Gwynne 2008; Kuntner et al. 2009a; Han et al. 2010; Carazo et al. 2011; Raveh et al. 2011; Takeshita et al. 2011). Empirical evidence, however, is still scarce.

Female resistance to mating/remating and sexual cannibalism are comparatively common in spiders (Elgar 1992; Schneider & Lubin 1998; Elgar & Schneider 2004; Prenter et al. 2006; Wilder et al. 2009; Schneider & Andrade 2011), where a variety of behavioural male traits may serve as counteradaptations. These include elaborate courtship displays (Elgar & Nash 1988), nuptial gifts during courtship (Albo & Costa 2010), opportunistic mating with feeding, hunting or moulting females (Moya-Larano et al. 2004; Fromhage & Schneider 2005), genital mutilation and plugging (Segoli et al. 2008; Nessler et al. 2009; Kralj-Fišer et al. 2011), mate guarding (Fromhage & Schneider 2005; Kralj-Fišer et al. 2011), abdominal constriction (Andrade et al. 2005) and mate binding, in which the male deposits fine silk onto the female's body in between

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copulation bouts (Bruce & Carico 1988; Kuntner et al. 2009b; Supplementary material: Fig. S1a, b and Video S1). Nevertheless, among all these male behavioural traits, to date there has been only experimental demonstration of opportunistic mating with feeding females (Moya-Larano et al. 2004; Fromhage & Schneider 2005) that reduces the male's risk of cannibalism and injury.

Mate-binding behaviour was first described by Robinson & Robinson (1980) in the nephilids *Nephila pilipes* (as *Nephila maculata*) and *Herennia papuana* (as *Herennia ornatissima*; see also Preston-Mafham & Preston-Mafham 1998; Kuntner et al. 2009b), but is apparently more widespread as it was recently also found in *Caerostris* sp. (M. Gregorič, personal communication). Kuntner et al. (2009b) hypothesized that mate binding was an obligatory component of the precopulatory repertoire in *N. pilipes*, but this, and its precise function, remains untested. Among the putative functions of mate binding, authors have suggested that it may serve as stimulation for the female (Robinson & Robinson 1980) or perhaps to counter female cannibalism (Kuntner et al. 2009b). Other authors simply assumed that mate-binding silk strands are saturated with sexual pheromones (Preston-Mafham & Preston-Mafham 1998). To date, no study has experimentally tested any of these hypotheses. Furthermore, the possibility of direct tactile communication between females and males during mate binding has also not been explored. We studied all aspects of mate binding in *N. pilipes*, a common tropical nephilid spider with extreme sexual size dimorphism and cannibalism (Kuntner & Coddington 2009; Kuntner et al. 2009b). We focused on the function of mate binding and the mechanisms by which males could reduce female aggressive tendency and calm females to facilitate copulations.

In our preliminary experiments in the laboratory, we observed that virgin *N. pilipes* males could successfully mate with a female on her web without first performing mate binding. After covering the male's spinnerets to prevent his laying of silk, we observed mate binding-like movements without silk being deposited, with males successfully mating multiply and exhibiting mate-binding behaviour whenever copulations were interrupted by aggressive females. These observations suggested that laying of silk per se was not essential during mate binding. Furthermore, the role of pheromones, if any, was questioned. In the present study, we determined whether male-produced chemical or tactile cues (or both) were responsible for rendering females less aggressive and allowing further copulations. We hypothesized that mate binding was not necessary prior to the first successful copulation, but that it was necessary for subsequent successful bouts. We also hypothesized that both tactile and chemical signals during mate binding were important. To test these two hypotheses, we conducted behavioural assays in the laboratory, in which we manipulated the means of chemical and tactile communication of *N. pilipes* females and males.

METHODS

Spiders and Maintenance

The experiments were conducted in the laboratory using spiders collected from Pulau Ubin in Singapore (1°24'30"N, 103°57'40"E). To manipulate spiders with known mating histories, females were collected as subadults (i.e. one moult away from adulthood) and reared until adulthood in the laboratory ($N = 162$). In the field, usually one to six adult males guard a subadult female in her web. Once the subadult female has reached maturity, males compete with each other to mate with the female (Robinson & Robinson 1980), and males rarely migrate from one web to another to search for new females unless local females go missing (S. C. Zhang, personal observation). Thus we collected all adult males ($N = 212$) from subadult females' webs and checked their palps before use.

Only males with intact palps (i.e. without any damage, see Kuntner et al. 2009b) were used in the experiments. In the laboratory, we kept females individually in plastic frames (50 × 50 cm and 10 cm high) with bamboo sticks attached to their inner sides to allow them to build complete orb-webs on which all mating trials were conducted. We destroyed the webs that had been built prior to maturity to ensure that females would build new webs after their final moult. All males were kept individually in foam-covered plastic vials (0.25 litres). All spiders were kept in the laboratory with controlled environmental conditions (temperature: 25 ± 10 °C; relative humidity: $80 \pm 10\%$; photoperiod: 12:12 h light:dark with lights on between 0800 and 2000 hours). Males were fed with house flies, *Musca domestica*, twice a week, while females were fed with mealworms, *Tenebrio molitor*, daily. Those spiders that were not subjected to treatments were released back to their original habitat.

Behavioural Definitions

During mating trials, we defined a female as being aggressive if she (1) shook her web and chased the male during his approach, (2) kicked the approaching male away when he touched her legs, (3) furiously shook her body when the male was mounting her dorsum, (4) forcefully flicked the male off and tried to grab him while he mounted her venter, (5) abruptly interrupted mating, trying to kick the copulating male off and grab him. If the female kept motionless and passive, we interpreted this as being less aggressive, or calm.

Function of Mate Binding

To examine whether mate binding was a necessary component of the male precopulatory repertoire and whether it could reduce female aggressive tendency and cannibalism, we performed mating trials in the laboratory on female webs. Each individual (male and female) was used only once and thus had no courtship and mating experience before the trial. We started each trial by gently placing a male on a female's web about 15 cm away from her, and recorded all occurrences and combinations of insertion, mate binding and cannibalism. If a male dismounted the female after she had aggressively interrupted the first insertion, the male was given 20 min to resume mating. We recorded whether the female became calm or cannibalized the male in the presence and absence of mate binding. Trials lasted 1 h. All interactions between the male and female were filmed by HD video cameras. *Nephila pilipes* males often mate opportunistically when the female is engaged in wrapping or consuming prey (Robinson & Robinson 1980; Kuntner et al. 2009b); therefore, no prey were provided to the females during the mating trials to control for the possibility of opportunistic mating, which would have reduced the occurrence and frequency of female cannibalism (Fromhage & Schneider 2005). Only trials in which males successfully mated (i.e. achieved their first insertion) were included in data analysis. A total of 30 successful trials were conducted.

Mechanisms of Mate Binding

To explore the mechanisms underlying mate binding, that is, to determine the roles of chemical and tactile communication, we carried out mating trials using manipulated spiders. Most chemoreceptors in spiders are located on the distal segments of appendages, for example tarsi and metatarsi (Foelix 1970; Foelix & Chuwang 1973; Barth 2002). Tactile communication between males and females during mate binding might occur on the female's dorsum, which is where the male performs his behaviour;

the female's dorsum also bears tactile receptors in *N. pilipes* (M. Seah & D. Li, unpublished data). Therefore, we performed two manipulations of the females by (1) covering the female's dorsum to block the possible tactile communication between the male and female (i.e. tactile receptors blocked: T–; [Supplementary material: Fig. S1c, d](#)) and (2) destroying chemoreceptors on the female's forelegs and palps to prevent potential chemical communication between the mates (i.e. chemoreceptors destroyed: C–). To block tactile receptors on the female's dorsum, we covered the dorsum with liquid super glue (Selleys, PTY Ltd, Australia, www.selleys.com.au) by gently applying a thin layer of glue on the dorsum of females using a fine brush. The glue dried in 15 s after coating. To minimize possible effects of glue odours on the behaviour of the manipulated spiders, we placed them in airy, open frames until the trials started.

To destroy the chemoreceptors on females' legs and palps, we soaked all appendages in 50 ml of 0.4 mol/litre of zinc sulphate ($\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$) that had been dissolved in 0.3% Triton-X for 6 min. This method has been reported to be effective in deinnervating the chemoreceptive hair sensilla on the antennae of the cricket *Teleogryllus oceanicus* (Balakrishnan & Pollack 1997) and the chemoreceptors on the palps and legs of the wolf spider *Pardosa astrigera* (Jiao et al. 2010). During 24 h of testing, we observed no behavioural changes in females after such treatments compared with untreated females, both groups building new webs and catching house flies. In addition, males ($N = 4$) showed similar courtship and mating tendencies towards treated and untreated females, suggesting the treatments to females did not influence courtship behaviour of the males.

Virgin females were assigned at random to one of four groups: in Group 1 (control), females were not treated (i.e. both tactile receptors and chemoreceptors were intact; T+/C+); in Group 2, the female's dorsum was covered with liquid super glue but its legs and palps were not treated with zinc sulphate (T–/C+) to test the effect of tactile communication alone on mate binding; in Group 3, the female's legs and palps were treated with zinc sulphate but her dorsum was not covered by glue (T+/C–) to determine the effect of chemical communication alone on mate binding; and in Group 4, the females received both treatments (T–/C–) to test the effects of both tactile and chemical communication on mate binding.

Virgin males were randomly assigned to either the treatment or control group. In the control group, male spinnerets were not coated with liquid super glue. The treated males were anaesthetized by CO_2 and their spinnerets coated carefully with liquid super glue ([Supplementary material: Fig. S1e, f](#)), which prevented their silk production (S–) during mate binding. We confirmed males' spinnerets had been covered successfully by shaking off the males from a wooden stick three times without observing any draglines (spiders always produce a dragline when falling).

To control for the possibility that glue odour may confound the outcomes of our experiments, we set up another control group, in which the posterior dorsal abdomen of the female was partly covered (about 1 cm^2) with super glue, and the dorsum of the male, but not the spinnerets, was partly covered (about 0.1 cm^2) with glue.

After manipulation, all males and females were given 12 h to adapt and recover. All trials were carried out within 12–24 h after the treatments.

We began each trial by gently placing a randomly selected male (i.e. it could produce silk freely or could not produce silk; S+ or S–) onto the web of a randomly selected female from one of the four female groups about 15 cm away from her. For each trial, we recorded the occurrence of male mate binding and the responses of the female and the actions of the male in 20 min after mate binding, if any. If the male could tread on the female's abdomen to mate with

her within 20 min during mate binding, we deemed her as successfully calmed. If the female was still aggressive (for definition, see above), and the male failed to tread on her abdomen for mating, we deemed her as not having been calmed. Observations and recordings were made with HD camcorders. Both females and males were used only once. Only the trials in which males had exhibited mate binding were considered as successful.

Data Analysis

We used a one-tailed sign test to analyse the data on the frequency of males that had exhibited mate binding in their first mating and the frequency of the mate-binding males that succeeded in calming the females to allow the second insertion. We used goodness-of-fit chi-square tests to analyse the data on the frequency of males that mated after mate binding. We performed Fisher's exact test to analyse data on the frequencies of female cannibalism for males that exhibited mate binding and those that had not. All chi-square tests were performed using Minitab 15 (Minitab Inc., State College, PA, U.S.A.). Binary logistic regression was used to determine possible effects of treatments (female treatments: tactile receptors blocked and chemoreceptors destroyed; male treatments: spinnerets blocked or not) on female responses (calmed or not) to male mate binding. Logistic regression was the preferred option, as it can analyse dependent variables with categorical outcomes (Field 2009). The output from this regression is expressed as the likelihood (also known as odds ratio, OR) that a particular outcome category (in relation to the reference category) will occur when a particular independent variable is present. Here, the analysis provided the OR for female behaviour (calmed or not) when a particular variable (female treatment or male treatment) was present. We performed one binary logistic regression to assess the associations between the independent (female and male treatments) and dependent (if the female was calmed or not) variables. An OR of more than one meant that the female response (calmed or not) to male mate binding was more likely to occur when a particular treatment was present, and an OR of less than one meant that the female response was less likely to occur when that treatment was present. When calculating the OR for each combination of predictor-dependent variables, binary logistic regression assumes that all other variables are constant. Logistic regression was performed using IBM SPSS Statistics 19 (SPSS Inc., Chicago, IL, U.S.A.).

RESULTS

Behaviour of Males and Females during Mate Binding

To perform mate binding, the male first mounted the dorsal abdomen of the female, aligned with her head down, trod quickly down to the carapace area, and then rubbed his spinnerets against her carapace in a circular fashion. After one to several rounds, the male usually lifted his spinnerets, retreated to the starting point and carried the silk threads there ([Supplementary material: Video S1](#)). The male then ritualistically touched the female's palps, seemingly to recheck her receptivity ([Supplementary material: Fig. S1g](#)). Should the female at this point not wave her palps or at least not at high frequency (more than 3/s), the male would proceed to her venter to copulate. Otherwise, he resumed mate binding, as described.

Function of Mate Binding

In 30 successful mating trials, only two males (6.7%) exhibited mate binding prior to the first insertion (one-tailed sign test:

$P < 0.001$), 23 males (76%) performed mate binding when their first copulation was interrupted by the female ($\chi^2_1 = 8.533$, $P = 0.003$) and 22 (96%) of the 23 mate-binding males succeeded in calming the females to allow their second insertion (one-tailed sign test: $P < 0.001$). Of 23 males that exhibited mate binding, only four (17.4%) were cannibalized, while of seven males that did not show mate binding after their first insertion was interrupted but instead tried to resume copulation, five (71.4%) were cannibalized (Supplementary material: Fig. S1h). This difference, however, was not statistically significant (Fisher's exact test: $P = 0.1$).

Mechanisms of Male Mate Binding

Direct binary logistic regression was performed to assess the effect of female and male treatments on female responses (calmed or not) to mate binding. The full model included two independent variables, female treatments (i.e. covering female tactile receptors and destroying female chemoreceptors) and male treatment (i.e. blocking male spinnerets). The model as a whole revealed a unique statistically significant treatment effect on female responses ($\chi^2_4 = 119.967$, $P < 0.001$) and correctly classified 89.2% of females that were or were not calmed. As shown in Table 1, both female treatments and male treatments were significant predictors of female aggressiveness (Fig. 1). Compared to the control (T+/C+), covering female tactile receptors alone (T-/C+) or blocking both female tactile and chemoreceptors (T-/C-) increased the likelihood that females were not calmed despite mate binding (T-/C+: OR = 65.614; T-/C-: OR = 341.96). However, destroying female chemoreceptors had no significant effect on the likelihood that females were not calmed compared to the control (OR = 0; Table 1). Glue odour also had no significant effects on the likelihood that females were not calmed compared to the control (OR = 0; Table 1). Compared to the control (S+), blocking male spinnerets (S-) increased the likelihood that females were not calmed (OR = 5.387; Table 1). The OR for females that were not calmed when both tactile and chemoreceptors of females were blocked (T-/C-; OR = 341.96) suggested that females remained aggressive despite the occurrence of mate binding mostly when both tactile and chemoreceptors of females were blocked. Of 39 females, 33 were not calmed despite mate binding (Fig. 1).

To determine the relative importance of chemical and tactile communication in reducing female aggressiveness during mate binding, we compared the frequencies of females that were calmed during mate binding between the groups (T-C+) and (T+C-). Significantly fewer females were calmed in the T-C+ group than the T+C- group regardless of whether male spinnerets were covered (S-: $\chi^2_1 = 20.99$, $P < 0.001$) or not (S+; $\chi^2_1 = 6.95$, $P = 0.008$; Fig. 1).

DISCUSSION

We provide empirical evidence that mate binding is not an obligatory precopulatory behavioural element for males to mate with virgin females in *N. pilipes* since only 6.7% of males exhibited mate binding before their first copulation with virgin females. As predicted, mate binding always occurred after females had interrupted copulations and became aggressive towards their suitors. Mate binding, then, greatly reduces female aggressiveness and thus facilitates subsequent copulations. Therefore, it may be seen as a counteradaptation to female resistance to repeated mating rather than to mating per se. Moreover, the percentage of males being cannibalized by females decreased through mate binding from 71.4% to 17.4%, suggesting that mate binding may reduce sexual cannibalism (Kuntner et al. 2009b). More importantly, our study revealed the mechanisms of mate binding by which males reduce female aggressiveness; that is, both tactile and chemical cues together play crucial roles in rendering females more prone to repeated mating and in reducing the risk of sexual cannibalism. This is the first experimental demonstration of the advantage of male mate binding in a context of sexual conflict over female resistance to repeated mating and cannibalism.

This study focused on elucidating the mechanisms of mate binding, which males employ to calm aggressive females. Our experiments showed that most of those females with both tactile receptors and chemoreceptors blocked were still aggressive despite the occurrence of mate binding (Fig. 1). This demonstrates that both tactile and chemical communication between the sexes is crucial for successful mate binding. Moreover, our results show that tactile cues are of higher importance for mate binding to render females less aggressive and less resistant to repeated mating. There are a few lines of evidence supporting this. First, during mate binding the tactile communication alone (T+/C-) could calm the females, even when female chemoreceptors were destroyed (Fig. 1). Second, blocking female tactile receptors alone greatly reduced the number of females that were calmed compared with the control group (T+C+S+). Third, fewer females were calmed during mate binding when female tactile receptors were blocked (T-/C+) compared with the group with only chemoreceptors blocked (T+C-).

Contrary to the popular literature speculating that *N. pilipes* males use contact sex pheromones in the silk laid on females during mate binding (Preston-Mafham & Preston-Mafham 1998), our results suggest this is unlikely; if pheromones are produced by males during mate binding then these are not contact but rather airborne. Males often use chemical cues in searching for mates (Gaskett 2007), and these cues can be perceived by males as volatile (airborne) pheromones at a longer distance or contact pheromones at a closer distance, such as on a female's web silk, or draglines or

Table 1
Binary logistic regression for testing the effects of female and male treatments on female aggressiveness (calmed: reference; not calmed: predicted) during male mate binding

Variable	B	SE	Wald	df	P	Odds ratio		
						Exp (B)	Lower	Upper
Female treatment								
T-/C+	4.18	1.11	14.33	1	<0.001	65.61	7.52	572.7
T+/C-	-17.57	6934	0	1	0.998	0	0	0
T-/C-	5.84	1.18	24.56	1	<0.001	341.96	34.02	3436.9
Glue odour	-16.61	11603	0	1	0.999	0	0	0
Male treatment (S-)								
S-	1.68	0.61	7.66	1	0.006	5.39	1.63	17.75
Constant	-4.60	1.12	16.80	1	<0.001	0.01		

Treatments: female's carapace covered to block tactile receptors: T-; chemoreceptors destroyed: C-; male spinnerets blocked: S-. T+/C+ (control in the female treatments) was used as reference for the female treatments; S+ (control in the male treatment) was used as reference for the male treatment. T-/C+: the treatment in which only the female's tactile receptors were blocked; T+/C-: the treatment in which only the female's chemoreceptors were destroyed; T-/C-: the treatment in which both tactile receptors and chemoreceptors of females were blocked; glue odour: the treatment in which glue was applied to the anterior ventral abdomen of the male and to the posterior dorsal abdomen of the female. Hosmer & Lemeshow test: $\chi^2_6 = 3.967$, $P = 0.784$; $R^2 = 0.532$ (Cox & Shell), $R^2 = 0.731$ (Nagelkerke).

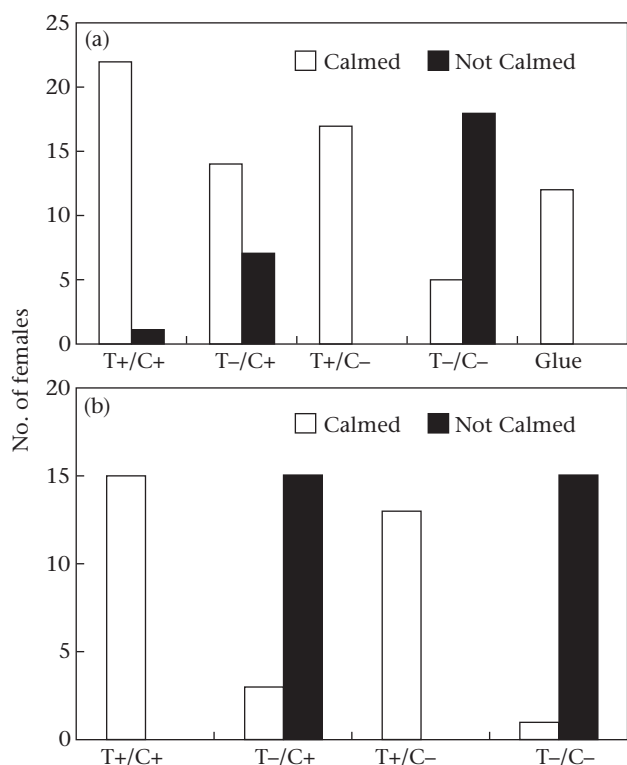


Figure 1. The number of females that were calmed or not in two male groups. (a) Male spinnerets were not blocked or control; (b) male spinnerets were blocked. T+/C+ control group: both tactile and chemical communication were not blocked; T-/C+ group: only the tactile receptors were blocked; T+/C- group: only chemoreceptors were blocked; T-/C- group: both tactile and chemoreceptors were blocked; Glue: the controls, which controlled for the effects of glue on mate binding.

on her body (Uhl & Elias 2011). Although female sex pheromones are common in spiders, male sex pheromones are also reported and used in various stages of mating. For example, the male black widow spider, *Latrodectus hesperus*, produces contact sex pheromones on its silk, which can be detected by chemoreceptors on the female's legs and palps (Ross & Smith 1979). On the other hand, the male desert spider, *Agelenopsis aperta*, produces airborne chemicals to induce temporary catalepsy in females during courtship, to increase his chance of successful copulation without being cannibalized (Becker et al. 2005). Likewise, male wolf spiders, *Allocosa brasiliensis* and *Allocosa alticeps*, produce volatile sex pheromones which induce female courtship behaviour (Aisenberg et al. 2010). A male-produced sex pheromone, (Z)-9-tricosene, used to increase males' copulation probability, was also identified in a pholcid spider, *Pholcus beijingensis* (Xiao et al. 2010). Our study is the first indication of the airborne male pheromones used to reduce female resistance to repeated mating and female cannibalism.

In addition, the fact that when the tactile receptors were blocked (T-C+S+ and T-C+S- trials) the percentage of females that were calmed varied from 16.7% when male spinnerets were covered (S-) to 66.7% when uncovered (S+) suggests that the effective, airborne male chemical signals might be produced from the spinnerets and adjacent regions. While no sexual pheromone glands have been identified in any spider, it would be worth examining *N. pilipes* male spinnerets or adjacent regions for the potential presence of such glands.

Silk deposition during the action of mate binding seems to be a by-product of tactile communication; instead, the action of moving around the dorsum of females with spinnerets rubbing against the dorsum appears to be important. In addition, our results

show that tactile communication is the most important in this process. Therefore, the definition of mate binding, where the male deposits fine silk on the dorsum of the female (Preston-Mafham & Preston-Mafham 1998; Kuntner et al. 2009b), could also be more descriptively termed 'mate massaging'.

Copulation duration has long been thought of as one of the most critical measures of male reproductive success (Simmons 2001). In general, copulation duration is positively related to sperm transfer, which may determine paternity, and thus males are expected to copulate for as long as possible. To enhance their paternity, males of many spider species attempt to prolong their copulation duration. For instance, copulation duration in *Argiope bruennichi* is reported to be directly related to sperm transfer and relative paternity success (Schneider et al. 2006). In our study, male *N. pilipes* performed mate binding after being rejected or interrupted by the female, and it appears that mate binding enables the male to mate with the female multiply, thus maximizing his paternity.

The present study is the first demonstration of the adaptive value of male mate binding through which males reduce female resistance to repeated mating and the risk of sexual cannibalism in *N. pilipes*. Such benefits may be achieved through both tactile and chemical communication between males and females during mate binding, but the former seems to be more important than the latter. Our results also suggest that silk deposition during mate binding may be a by-product of tactile communication and that the pheromones used may be airborne and produced from male spinnerets or adjacent regions. In conclusion, mate binding may have evolved as a male counteradaptation in a context of sexual conflict over female resistance to repeated mating and the risk of sexual cannibalism.

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Supplementary Material

Supplementary material associated with this paper is available, in the online version, at doi:10.1016/j.anbehav.2011.09.010.

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