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Sexual conflict and arms races between the sexes: a morphological adaptation for control of mating in a female insect

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SUMMARY

Conflict between the sexes over control of copulation may drive the coevolution of elaborate genitalia and other secondary sexual structures. Support for this hypothesis is limited to male adaptations that function to enhance male control over females in copulation (e.g. structures that function to clasp females). Evidence for morphological adaptation in females is critical to the hypothesis, yet lacking. Here, we present the first experimental evidence demonstrating that female abdominal spines in water striders function to increase female control over copulation. By experimentally extending the phenotypic size range of these spines, we show that this morphological adaptation, specific to females, allows them to thwart harassing males, and as a result, reduce the frequency of costly matings to females. This demonstrates the coevolutionary nature of sexual conflict and that females are indeed active participants in the evolutionary conflict over control of reproduction.

1. INTRODUCTION

Coevolutionary models of sexual conflict predict adaptation and counter-adaptation by the sexes in a battle to control the outcome of sexual encounters (Parker 1979, 1984; Hammerstein & Parker 1987). In conflicts over the mating decision, elaboration of genitalia and secondary sexual structures may be one outcome of such coevolutionary arms races (Eberhard 1985). Male structures that improve male mating success at a cost to females have been documented in several species. For example, many insects possess claspers that enhance male control of copulation (Thornhill & Alcock 1983; Wing *et al.* 1983; Thornhill 1984; Arnqvist 1989*a*; Sakaluk *et al.* 1995). Although some female structures have been suggested to function as counter-adaptations (Pratt 1979; Robertson 1985; Cordero 1992; East *et al.* 1993; Cook *et al.* 1994), experimental evidence is lacking (Fincke 1994*a, b*). This has been used as evidence against this coevolutionary pathway (Eberhard 1985). Elucidation of the functional morphology of any such traits in females is thus key to our understanding of the evolutionary dynamics of sexual conflict (Sakaluk *et al.* 1995).

The mating system of many water strider species (Heteroptera: Gerridae) is characterized by intense sexual conflict over mating decisions (Rowe *et al.* 1994; Spence & Andersen 1994; Arnqvist 1995). Males

frequently pounce on females and attempt to grasp them. Females respond to this with a vigorous premating struggle and try to dislodge the males. During this premating struggle, males attempt to secure an anterior and a posterior grasp of the female, with their forelegs and genitalia, respectively. These two points of attachment are critical to subdue reluctant females, and males of several species also possess abdominal claspers and spines on their forelegs that help grasp females (Arnqvist 1995). Both superfluous mating and male harassment are costly to females, because they drastically increase predation risk and energetic expenditure (Wilcox 1984; Arnqvist 1989*b*; Fairbairn 1993; Rowe 1994). Females adjust their reluctance during premating struggles to balance these costs imposed by males (Arnqvist 1992*a*; Rowe 1992). Any female structure that would increase the ability of females to resist males during premating struggles would decrease the overall cost to females imposed by males: by decreasing the cost of repelling males and by decreasing the frequency of superfluous matings.

In the genus *Gerris*, females of some species have highly modified abdominal spines that are elongated and/or recurved over the genital segments (see figure 1). This is a derived state within the Gerridae, and these modifications are confined to females (Andersen 1993). We hypothesized that the modified spines function to decrease the ease with which males can achieve genital contact, and thereby posteriorly grasp the female during the premating struggle. Males rapidly eject their genitalia and bend them downwards,

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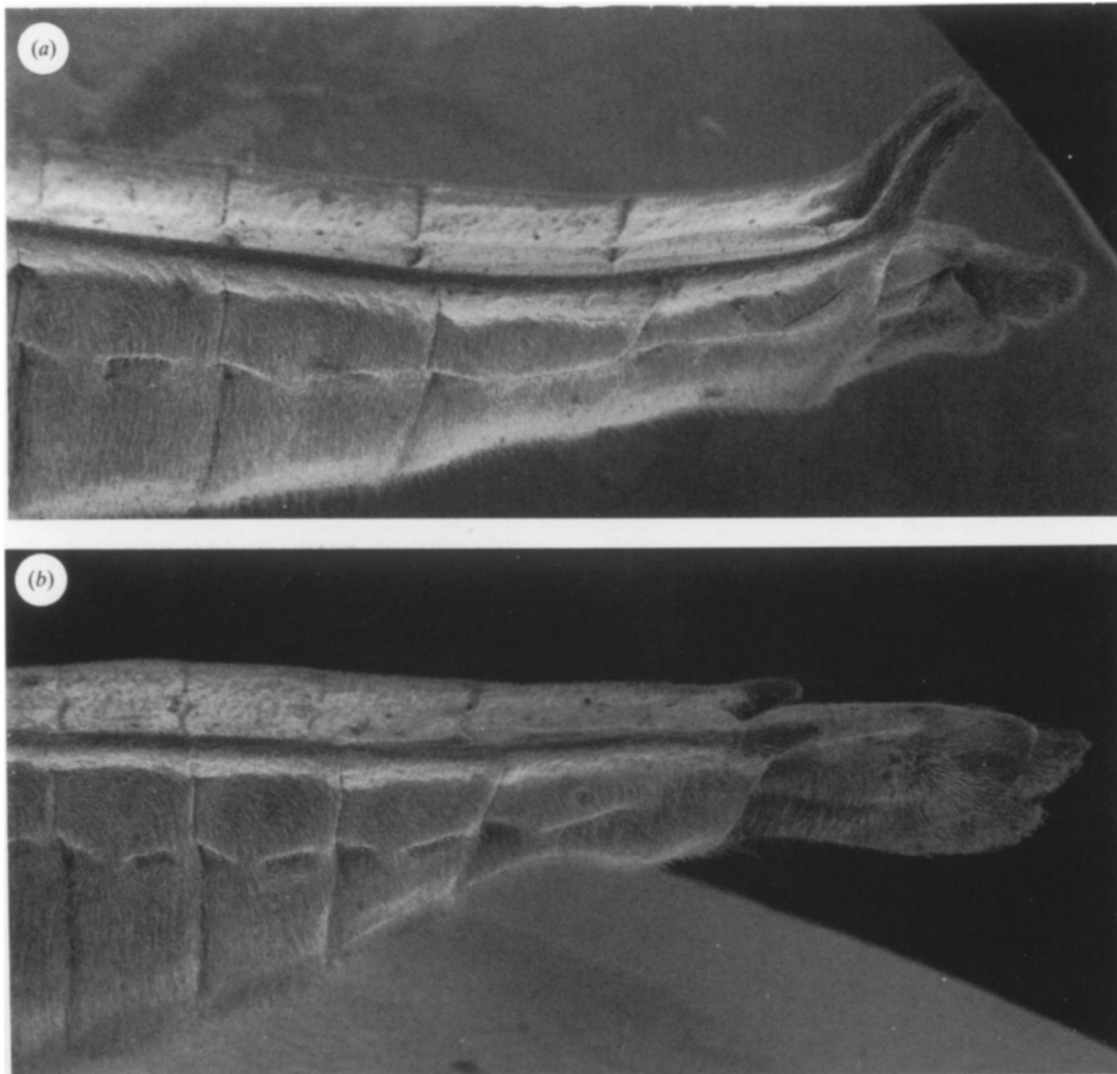


Figure 1. Scanning electron micro graph of a female (a) and male (b) *Gerris incognitus*, showing the elaboration of abdominal spines in females relative to males. The female spines in this species and several others are highly modified (elongated and/or curved over the genital segments) relative to the original character state found in most species in the genus and in outgroups (Andersen 1993).

attempting to clutch the tip of the female abdomen. The modified female spines increase the posterior distance between the abdomens of the sexes during the premating struggle, impeding the male's critical genital grasp. Thus, we predict that the time taken for females to thwart males during the premating struggle, is a decreasing function of the length of spines. As a result, we also predict that the mating frequency of females is a decreasing function of spine length. In contrast, we expect no effect of spine length on the durations of the copulation or mate guarding phases, because these stages occur after genital contact is made.

2. METHODS

All experiments reported here were performed with *Gerris incognitus*. In this species, spines are greatly elongated and elevated in females (see figure 1): the abdominal spines constitute 6.2% ($n = 12$, s.d. = 0.46) of the total body length in females but only 3.0% ($n = 12$, s.d. = 0.64) in males (ANCOVA of spine length on body length, with sex included as a categorical covariate; effect of sex: $p < 0.001$), and the angle between the axis of the spines and the main body axis

(in lateral view) average 31.1° ($n = 30$, s.d. = 5.3) in females and 6.2° ($n = 30$, s.d. = 5.1) in males (ANCOVA of spine angle on body length, with sex included as a categorical covariate; effect of sex: $p < 0.001$). For our laboratory experiments, water striders were captured on 11 May 1994, from a natural population in the Bosque del Apache Wildlife Refuge, New Mexico, U.S.A.

We manipulated the length of the abdominal spines of female *G. incognitus* under a dissecting microscope, to create three groups of females: those with lengthened, shortened, and normal spines ($n = 32$ in each). In the first, spines were lengthened by means of resin glue (used to mark domestic bee-queens) to approximately 1.5 times their original length. In the second, spines were shortened to approximately 0.5 times their original length by removing the proximal part of the spines with a pair of micro-scissors. The spines of the third group were left unmanipulated. While several potential control treatments are theoretically possible (e.g. shortening the spine and lengthening with glue to its original length, or removing and reattaching the proximal part of the spine), leaving the spines unmanipulated controls not only for spine length, but also for any confounding effects that spine manipulation *per se* might have. In the second and third treatment groups, tiny droplets of resin glue were also placed on the sides of the abdomen, to control for any confounding

chemical effects that might result from the resin glue itself. All individuals used in the experiments described below were individually marked and fed *ad libitum* with frozen fruitflies and field crickets.

Two experiments assessed the functional significance of the abdominal spines. In the first, we determined the effect of spine length on female attractiveness to males and on the ability of females to thwart males during the premating struggle. The pool of males used in these trials consisted of 20 males held individually in 8 cm diameter plastic containers. Females ($n = 20$) from each of the three treatment groups were individually introduced to a randomly selected male, and the time elapsed before the first mating attempt was recorded (± 0.05 s). For each first mating attempt, the time elapsed between when the male attained mating position on top of the female and when the male was dislodged by the female, was recorded directly with a stopwatch (± 0.05 s) to provide a measure of premating struggle duration. To reduce variance caused by intermale variation, the experiment was repeated with a second male, and the average durations of the two quantities for the different males were used as measures of each female's: (i) attractiveness to males; and (ii) ability to dislodge harassing males.

In a second experiment, designed to assess the effects of spine length on mating patterns, one female from each of the three treatment groups and five randomly selected individually marked males were introduced into each of twelve plastic pools (25 cm \times 30 cm). During five consecutive days following a two-day acclimatization period, a series of spot checks was performed in each of the pools, once every 10 min between 10.00 h and 18.00 h. At each check, we recorded all matings, and whether the pair was copulating or mate guarding. This allowed us to analyse the effects of spine length on mating frequency as well as copulation, guarding and total mating duration.

In the second experiment, we also calculated the variance in male mating success for each female, based on individual mating histories. This measure provides an estimate of the opportunity for sexual selection. Variance in male mating success is principally composed of variance resulting from male–male competition, female choice and random error. Given that the sex ratio did not vary, and that an effect of female spine length on male–male competition is highly unlikely, the contribution of male–male competition should be constant across female treatments. Any variance across female treatments should therefore be a result of variation among females in their ability to exercise choice, which allow us to test for effects of spine length on female mate selectivity. Female choice is known to be an important form of sexual selection in water striders (Arnqvist 1995).

All statistical analyses reported in this paper were performed with the SYSTAT statistical package (Wilkinson 1992; Kirby 1993).

3. RESULTS

There was a highly significant, overall effect of spine length on a female's ability to dislodge harassing males (see figure 2*a*; one-way ANOVA on log-transformed data; $F_{2,57} = 18.43$, $p < 0.001$). Males were dislodged in all observed mating attempts, but females with lengthened spines dislodged males more rapidly than females with normal spines, and females with normal spines dislodged males more rapidly than females with shortened spines (group differences tested with Tukey post-hoc comparisons; lengthened versus normal, $p = 0.031$; normal versus shortened, $p = 0.003$). Further-

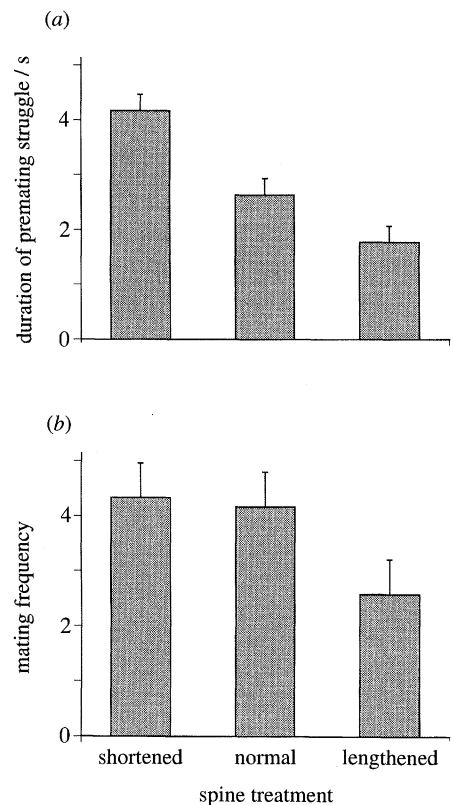


Figure 2. The effects of the experimental manipulation of female lateral spine length on mating behaviour and mating pattern. (a) The mean ($n = 20$, +s.e.) premating struggle duration of females with shortened, normal and lengthened abdominal spines in the first experiment. (b) The mean ($n = 12$, +s.e.) number of observed matings during five days for females in the three treatment groups in the second experiment.

more, the effect of spine length on struggle duration was linear rather than quadratic (single degree of freedom polynomial contrasts; test of linear trend, $F_{1,57} = 36.63$, $p < 0.001$; test of quadratic trend, $F_{1,57} = 0.23$, $p > 0.5$). There was no effect of spine length on females' attractiveness to males, measured as the time elapsed before the first mating attempt (one-way ANOVA on log-transformed data; $F_{2,57} = 1.39$, $p = 0.256$).

The results of the second experiment were analysed by within-subjects (repeated measures) ANOVA on log-transformed data, treating pools as subjects, and spine length as the subject's factor. Spine length had a significant overall effect on the number of observed matings (see figure 2*b*; $F_{2,22} = 5.46$, $p = 0.012$). Females with lengthened spines mated less frequently than females with normal spines, whereas the mating frequency of females with normal and shortened spines did not differ significantly (group differences tested with planned post-hoc contrasts; lengthened versus normal, $F_{1,11} = 8.74$, $p = 0.013$; normal versus shortened, $F_{1,11} = 0.05$, $p > 0.05$). However, there was no evidence for a quadratic, rather than a linear, decrease in mating frequency with increased spine length (single degree of freedom polynomial contrasts; test of linear trend, $F_{1,11} = 12.10$, $p = 0.005$; test of quadratic trend, $F_{1,11} = 2.55$, $p = 0.139$). Furthermore, there were no significant effects of spine length on

either copulation duration, mate guarding duration, total mating duration or female mate selectivity ($F_{2,22} = 1.55$, $p = 0.24$; $F_{2,22} = 0.29$, $p > 0.5$; $F_{2,22} = 0.23$, $p > 0.5$; and $F_{2,22} = 1.14$, $p = 0.34$; respectively).

4. DISCUSSION

The results of our experiments support our hypothesis that these spines function to increase female control over copulations and to reduce the overall cost of mating interactions with males. Most importantly, the direct behavioural observations revealed that the duration of premating struggles decreased significantly with each incremental increase in spine length, demonstrating that a female's ability to thwart harassing males is directly related to spine length. Spine length also had a corresponding overall negative effect on female mating frequency, but, as predicted, there were no significant effects of spine length on either copulation, guarding or total mating duration. Three lines of evidence also show that changes in male behaviour did not cause these results. First, spine treatment in females did not affect the time before male initiation of mating attempts. Secondly, males did not alter either copulation or guarding duration, depending on female spine length. Third, the treatment effects were related to female spine length rather than deviation of spine length from normal (i.e. the effects were linear rather than dome shaped), as would have been expected if male behaviour had been affected by spine manipulation *per se*.

The lack of a significant difference in mating frequency between females with shortened and normal spines in the post-hoc comparisons, suggests that the effect of spine length on mating frequency may be non-linear. However, we have no indication that this was the case; there was an overall significant linear relation, but no significant nonlinear trend.

It has been argued that premating struggles in insects may promote female choice of males with 'good genes', in addition to reducing costly mating (Thornhill & Alcock 1983; Arnqvist 1992*a*; Sih & Krupa 1992; Rowe 1994; Rowe *et al.* 1994). Female abdominal spines could therefore also serve to facilitate adaptive female mate choice. Under this hypothesis, females with long spines should be more able to exercise choice than females with short spines. However, the fact that our experimental manipulation of the spines had no effect on the variance in male mating success, does not support this suggestion.

Our results demonstrate that the modified abdominal spines function to decrease the time required to thwart unwanted mates, and thereby increase female control over mating decisions and decrease the overall cost of harassment by males. Previous studies of related species show that females balance the various costs of mating (Arnqvist 1992*a, b*; Rowe 1992, 1994; Sih & Krupa 1992). By reducing the time and thus the cost of repelling males, spines reduce the cost of remaining single in the face of repeated harassment. The striking of a new balance by females with longer spines is most likely reflected in the observed reduced mating frequency. Therefore our results also provide a new

line of evidence for the hypothesis that mating dynamics in this group closely reflect the economic interests of females (Rowe *et al.* 1994).

Water strider mating systems provide a strong case for the coevolutionary scenario predicted by hypotheses based on sexual conflict (Parker 1979, 1984; Walker 1980; Knowlton & Greenwell 1984; Eberhard 1985; Hammerstein & Parker 1987; Gowaty 1994). Under these hypotheses, adaptation and counter-adaptation by males and females to control mating decisions are expected to evolve in a coevolutionary arms race. Male water striders have evolved various forms of clasping devices to overcome female resistance (Arnqvist 1995) and, as demonstrated here, females possess morphological adaptations to aid in rejection of unwanted mates. These results are novel and important to our understanding of the evolutionary dynamics of sexual conflict, because it has been suggested that such adaptations in females may not exist (Eberhard 1985). We have shown that sexual conflict may indeed drive the evolution of secondary sexual morphological traits in females.

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