

## Mate guarding and sperm displacement in the water strider *Gerris lateralis* Schumm. (Heteroptera: Gerridae)

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**SUMMARY.** 1. Field and laboratory observations on the mating behaviour of *Gerris lateralis* Schumm. allowed three distinct phases to be distinguished: (i) a precopulatory phase (1.5 min, SD=1.3), (ii) copulation (16.2 min, SD=12.9), and (iii) a postcopulatory phase. The duration of the postcopulatory phase, during which the male rode passively on the back of the female without genital contact, varied considerably (11 min to >48 h). Females appeared reluctant in all matings, and matings were forced by males.

2. Laboratory experiments showed that the females were able to store sperm for more than 30 days without decrease in fertilization rate. In double mating experiments, where partially sterilized males were used, it was demonstrated that sperm displacement was extensive. The last male to mate fertilized approximately 80% of the eggs.

3. It is concluded that the postcopulatory behaviour is beneficial to males in terms of paternity assurance, and it is interpreted as a mate guarding behaviour.

### Introduction

The traditional view of sexual selection theory holds that females invest more in offspring production than do males. Females are generally thought to be limited in their reproductive success primarily by the number of gametes they produce. Males are thought to be less restricted by their number of gametes, but rather their fitness is limited by the number of matings they undertake. Males should therefore try to maximize their number of copulations (Darwin, 1871; Bateman, 1948; Krebs & Davies, 1981). However, males of many arthropod species have evolved behavioural patterns which prevent other males from get-

ting access to the female. These behaviours (e.g. prolonged copulation, passive phases during copulation and pre- and postcopulatory mate guarding) require time and/or energy that could have been used in finding and mating with other females. Thus males incur costs while guarding, and it seems logical to assume counterbalancing benefits to be important for these behaviours to persist.

The phenomenon most often used to explain behavioural traits such as mate guarding is sperm displacement, which has been shown to occur in several insect species (e.g. Parker, 1970a, b, c; Riemann & Thorson, 1974; Sillén-Tullberg, 1981; Thornhill & Alcock, 1983; Fincke, 1984; Gwynne, 1984; Parker, 1984). Its effects in insects is that the last male to mate with a female fertilizes the major proportion of the eggs. The previously mentioned

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behavioural patterns can thus be seen as adaptations to reduce sperm competition by preventing other males from mating with the same female (e.g. Parker, 1970a, c; Mason, 1980; Sillén-Tullberg, 1981; Fincke, 1984). Thus, the optimal male strategy in many insect species is not to mate with as many females as possible but rather to prevent sperm displacement by other males (Parker, 1970a, b, c, 1974; Mason, 1980). Males can assure paternity by protecting their sperm investment either mechanically, chemically or behaviourally (Parker, 1970b; Fincke, 1984).

While multiple matings are beneficial to males, they may constitute a cost to females. However, there are several hypothetical female benefits associated with multiple matings (cf. Walker, 1980; Thornhill & Alcock, 1983; Gwynne, 1984). For example, females of some insect species have been shown to use additional matings to replenish depleted sperm supplies, thereby increasing their level of fertility (Boorman & Parker, 1976; Thornhill & Alcock, 1983).

The habit of the male riding passively on the back of the female after copulation is widespread among the semi-aquatic insects (cf. Sattler, 1957; Andersen, 1982). Several studies discuss mating behaviour and the selective advantages of postcopulatory guarding in water striders. However, the topic lacks detailed information, and no results concerning sperm longevity and displacement within these insects have been published.

In this paper I describe the reproductive behaviour in *Gerris lateralis*, and examine aspects such as sperm longevity and displacement. *G. lateralis* has a mainly boreo-alpine distribution, and it lives preferentially in small streams and various types of pits (Vepsäläinen, 1973). *G. lateralis* overwinters on land as an imago in a prereproductive state. Reproductive activity begins in the spring after a period of gonad maturation following diapause termination (Vepsäläinen, 1978; Andersen, 1982).

## Methods

Apterous adults of *G. lateralis* were collected soon after the termination of their diapause, between 14 and 17 May 1986. The collection

site was the outlet of the River Tavleån, 8 km SE of Umeå in northern Sweden (63° 47'N, 20° 35'E). Observations on mating behaviour were made at the collection site. In the laboratory the water striders were placed in circular containers (1.0 m diameter) and fed with frozen *Drosophila melanogaster* in a 20 h light:4 h dark regime and at 20±1°C. The sexes were kept separated and the food was held superabundant until the start of the experiments. Pieces of floating styrox were used as oviposition sites.

In the first experiment ten males and ten females were individually marked with enamel paint. The males and females were simultaneously introduced into a 20×30 cm plastic bowl, and the duration of the different phases in each mating was recorded ( $n=50$ ).

To ascertain whether females were able to store sperm for longer periods, eggs from two different groups were collected. One group of ten females was kept together with ten males for 34 days. The second group of ten females was kept with ten males for 2 days and then isolated from males for 32 days. Egg batches from the two groups were collected on nine occasions during the experiment, and the numbers of viable eggs were recorded. Viable eggs were defined as those which changed colour from white and opaque to yellowish brown within 2 days (Sattler, 1957; Andersen, 1982). By then the eyes of the embryo were visible as a pair of reddish spots. Food was held superabundant during this experiment.

Possible sperm displacement was investigated using females mated with normal and sterilized males. Seventy males were exposed to cobalt-60 gamma rays at a dose rate of 1.56 Gray min<sup>-1</sup> for 64 min, resulting in a total dose-rate of 100 Gray (10.0 krad). The males used in the experiment had been isolated from females for at least 10 days prior to sterilization, and each male was allowed to mate only once. Four types of matings were arranged: two controls with females subjected to double copulations with normal (N) or irradiated (I) males, respectively. In the two experimental double copulations, fifteen females mated first with a normal and then with an irradiated male, while another fourteen females copulated in reverse order. All copulations took place within 3 h of male irradiation. After copulation the females were isolated indi-

vidually in 11 cm diameter glass jars. After 7 days the egg batches were removed, their development followed and the number of viable eggs recorded. The females were fed with frozen red ants (*Formica rufa*), each female receiving one ant per day throughout the experiment.

## Results

No territoriality, courtship or intra-sexual aggression occurred during mating behaviour of *G. lateralis*. Males approached not only females but all objects that moved on the water surface, frequently attempting copulations even with other males. Males grasped a female without prior courtship. During mating the male maintained position on top of the female by clasping her thorax with his forelegs and by folding the midlegs around the middle femora of the female. The mating that followed could be divided into three distinct phases: (i) precopulatory phase, (ii) copulation, and (iii) postcopulatory phase. During the precopulatory phase, which averaged 1.5 min (SD=1.3,  $n=50$ ), the male tried to obtain genital contact while the female attempted to throw him off. The female often raised her midlegs and thereby her body until they both tipped over backwards to a position upside down on the water surface. Females succeeded in 18% of their throw-off attempts ( $n=50$ ). Copulation started when genital contact was attained. During copulation the throw-off attempts of the females stopped

almost completely. The copulation averaged 16.2 min (SD=12.9,  $n=41$ ), terminating when genital contact ceased. The duration of the postcopulatory phase, during which the male rode passively on the back of the female without genital contact, varied considerably. In 78% ( $n=41$ ) of the matings it lasted for more than 1 h, though it ranged between 11 min and more than 48 h. Females regularly made throw-off attempts during this phase, and in all matings where termination was recorded ( $n=9$ ) the males were thrown off. Both females and males mated many times during the experiment.

In the sperm longevity experiment females isolated from males had a frequency of viable eggs of more than 90% after 32 days of isolation. The proportion of viable eggs was not significantly lower than for females kept with males (contingency table test,  $\chi^2$  (df=8)=11.49,  $P>0.05$ ).

Sperm displacement was estimated from the four types of double matings. In viable eggs were found in matings with normal (N-N) and viable eggs in matings with irradiated males (I-I) (Table 1). However, the frequencies of viability in I-I and I-N matings differed significantly from each other as did the frequencies of viability in N-N and N-I matings (Table 1). The degree of sperm displacement,  $x$ , in I-N matings was thus estimated as a linear average of separate viabilities in the N-N and I-I matings (Sillén-Tullberg, 1981):

$$a = bx + c(1 - x)$$

where  $a$  is the mean frequency of viable eggs in

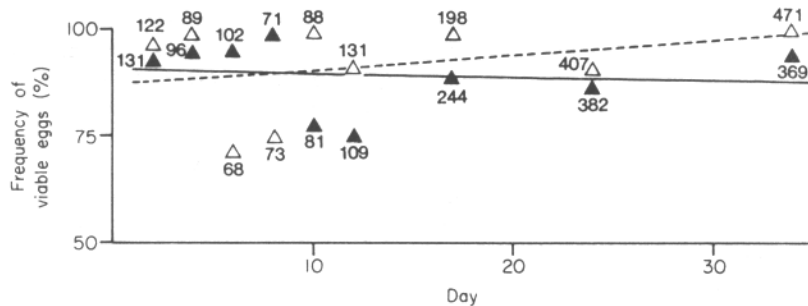


FIG. 1. Frequencies of viable eggs in females kept with and without males, respectively. Unfilled triangles and dashed line represent females ( $n=10$ ) kept with males ( $n=10$ ) ( $y=0.314x+87.4$ ,  $r=0.291$ , NS). Filled triangles and solid line represent females ( $n=10$ ) isolated from males ( $y=-0.095x+90.1$ ,  $r=-0.119$ , NS). Numbers represent the number of eggs in each observation.

TABLE 1. Number of eggs and frequencies of viable eggs in females subjected to double matings with normal (N) and irradiated (I) males, respectively. *P* values calculated by Mann-Whitney *U*-test.

Mating sequence	No. of females mated ( <i>n</i> )	No. of eggs per female		Frequency of viable eggs (%)		Significance of difference in viability
		$\bar{x}$	SD	$\bar{x}$	SD	
I-I	14	45.6	14.7	72.9	17.0	
I-N	14	41.1	14.2	89.5	9.9	<i>P</i> <0.05
N-I	15	46.4	12.1	77.0	10.9	<i>P</i> <0.05
N-N	15	42.5	10.7	93.1	6.7	<i>P</i> <0.05

I-N matings, and *b* and *c* are the mean frequencies of viable eggs in N-N and I-I matings, respectively. The degree of sperm displacement in N-I matings was estimated as a linear average of inviable eggs in I-I and N-N matings. In this case, *a* is the mean frequency of inviable eggs in N-I matings, and *b* and *c* are the mean frequencies of inviable eggs in I-I and N-N matings, respectively. The estimate of sperm displacement was 82.2% in the I-N matings and 79.7% in the N-I matings. The experiment thus showed that the last male to copulate with a female fertilized the predominant part of the eggs. The overall magnitude of sperm displacement was approximately 80%.

The mean number of eggs per female did not differ significantly between the four groups of females in the sperm displacement experiment (one-way ANOVA,  $F=0.52$ ,  $P>0.05$ ). The pooled mean number of eggs per female was 43.9 (SD=12.9,  $n=58$ ), a figure corresponding to 6.3 eggs per female per day.

## Discussion

Males of *G. lateralis* appear non-selective in their choice of potential mates. Matings appeared to be forced by males, and the terms 'ardent males' and 'reluctant females' seem relevant for the behaviour. The mating behaviour appears uncomplicated relative to that of some other species within the Gerridae where territorially, alternative mating tactics and courtship occur (e.g. Wilcox, 1972; Rubenstein, 1984; Hayashi, 1985; Vepsäläinen & Nummelin, 1985; Spence & Wilcox, 1986).

Females of many insect species are able to store sperm in the spermatheca for longer or

shorter periods (Andersen, 1975; Mason, 1980; Thornhill & Alcock, 1983). It has previously been demonstrated that the physiological qualifications for sperm storage exist in Gerridae (Pendergast, 1957; Andersen, 1982). In this study I show that females of *G. lateralis* are functionally able to store sperm for more than 30 days, and that there is no decrease in fertilization rate within this period. Since the reproductive period of water striders at these latitudes lasts approximately for 2 months (Vepsäläinen, 1974), it is likely that one or a few matings are sufficient to provide a female with enough sperm for her total egg production. Hence, the females do not seem to gain anything from multiple matings in terms of increased fertilization rates. This fact, combined with potential disadvantages such as increased exposure to predators, decreased foraging efficiency and increased energetic costs when carrying the male (Andersen, 1982; Wilcox, 1984), might explain the reluctance of females to mate. Multiple mating and post-copulatory guarding in *G. lateralis* might thus represent sexual conflicts of interest. However, no quantifications of reluctance for different categories of females were made, and there might be situations, as for example a strongly male-biased operational sex ratio, in which multiple matings and guarding may be beneficial for the females (cf. Thornhill, 1976; Andersen, 1982; Wilcox, 1984). Female reluctance could also be seen as a means of female choice. Female fitness might increase if only males which are able to resist female throw-off trials are allowed to mate, if this ability is inherited by the offspring.

Vepsäläinen & Patama (1983) found the daily egg production per *G. lateralis* female to be 4.5 (26°C) and 4.1 (17°C). The value

calculated here in the sperm displacement experiment (6.3 eggs per day and female, 20°C) was considerably higher. However, the daily egg production is not likely to be constant over the total reproductive period. This could in part explain the difference in daily egg production. It is notable that the frequency of viable eggs was approximately 90% under normal conditions. This value is consistent with the frequency of viable eggs found by Matthey (1976) in *Gerris remigis* Say (85%) and by Spence (1986) in *Gerris buenoi* Kirkaldy (90%).

Sperm displacement occurs in *G. lateralis*, and the last male to copulate fertilizes approximately 80% of the subsequent egg production. The degree of sperm displacement is of the same magnitude as in several other insect species (e.g. Parker, 1970b; Riemann & Thorson, 1974; Sillèn-Tullberg, 1981; Fincke, 1984; Gwynne, 1984; Parker, 1984). Males of *G. lateralis* seem particularly resistant to gamma radiation. In studies of other insect species where a dose rate of 10.0 krad have been used, the males have shown a higher degree of sterility. However, when calculating sperm displacement as a linear average it is not the degree of sterility that determines the accuracy of the estimate, but the standard error of the means for the different mating categories used in the calculation.

Male postcopulatory guarding behaviours have typically been interpreted as paternity assurance mechanisms. An alternative hypothesis is that a male provides benefits to the female and ultimately his offspring by guarding, primarily by preventing conspecific males from disturbing the female (Gwynne, 1984; Thornhill, 1984). However, in polyandrous species such as *G. lateralis*, a male is unlikely to gain in terms of fitness by providing the female with benefits. An increase in female fitness (for example expressed as larger egg batches) resulting from guarding by a specific male, will most likely occur after a relatively long period of time, during which the female is likely to remate with other males. Further, females should not be reluctant during the postcopulatory guarding phase if they benefit by guarding. The postcopulatory behaviour of *G. lateralis* males, and possibly that of most other water strider species, should thus be interpreted primarily as a paternity assurance

behaviour. Males obviously have a lot to gain in terms of increased paternity by guarding females. Sperm displacement may thus have resulted in sexual selection favouring males which by guarding the female reduces the risk of their sperm being displaced by that of other males.

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