Behavioral Ecology Vol. 10 No. 4: 358–365

Postmating sexual selection: the effects of male body size and recovery period on paternity and egg production rate in a water strider

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The role of male body size in postmating sexual selection was explored in a semiaquatic insect, the water strider *Gerris lateralis*. To separate effects of male size per se from those due to numeric sperm competition, male recovery period (shown here to be proportional to ejaculate size) was manipulated independently of body size in a factorial experiment where virgin females were mated first with sterile males and then with focal males. Both relative male fertilization success and female reproductive rate were measured. The number of sperm transferred increased with male recovery period, an effect that was mediated by longer copulation duration, but there were no effects of body size on ejaculate size. Neither male size nor recovery period had any significant direct effects on male fertilization success. However, copulation duration influenced relative fertilization success, suggesting that males able to transfer more sperm also achieved higher fertilization success. Females exercised cryptic female choice by modulating their reproductive rate in a manner favoring large males and males that were successful in terms of achieving high relative fertilization success. Thus, successful males gained a twofold advantage in postmating sexual selection. This study has important implications for previous estimates of sexual selection in this group of insects because pre- and postmating sexual selection will be antagonistic due to limitations in male sperm production: males mating frequently (high mating success) will on average transfer fewer sperm in each mating and will hence tend to fertilize fewer eggs per mating (low fertilization success). *Key words:* body size, copulation duration, cryptic female choice, ejaculate size, *Gerris lateralis,* recovery period, reproductive effort, sexual selection, sperm competition, sperm precedence, water striders. *[Behav Ecol 10:358–365 (1999)]*

Our understanding of sexual selection and the evolution of mating systems is currently being significantly revised. Empirical and theoretical studies have by tradition dealt almost exclusively with variance in mating success among males as the generator of differential reproductive success and hence sexual selection (see Andersson, 1994), but many authors now stress the potential importance of variance in postmating paternity success among males for the evolution of sexual characters (Arnqvist, 1998; Briskie et al., 1997; Eberhard, 1985; Harcourt et al., 1981) as well as mating systems (Birkhead and Møller, 1992, 1993; Choe and Crespi, 1997; Eberhard, 1996). Although the principal importance of postmating sexual selection has been recognized since the 1970s (Lloyd, 1979; Parker, 1970; Smith, 1984; Thornhill, 1983), current knowledge of the causes and effects of variation in paternity success among males is very limited (Birkhead and Møller, 1992; Conner, 1995; Eberhard, 1996; Hosken and Stockley, 1998; Lewis and Austad, 1990; Simmons and Parker, 1992).

Nonrandom fertilization success among males can occur as a result of either competition between male gametes over fertilization (i.e., sperm competition; Parker, 1970; Smith, 1984), or as a result of any of a number of female processes that affect relative male paternity success (i.e., cryptic female choice; Eberhard, 1996; Lloyd, 1979; Thornhill, 1983). It has proven difficult to distinguish empirically between these two mechanisms, especially as they are not mutually exclusive (Bissoondath and Wiklund, 1997; Simmons and Parker, 1992; Simmons et al., 1996; Wilson et al. 1997; Wirtz, 1997). Models of sperm competition are typically based on some form of numerical competition, where the relative success of a male is a function of the number of sperm transferred by that male (Parker, 1990; Parker and Simmons, 1991, 1994; Parker et al., 1990). There are at least two different ways in which females can exercise cryptic female choice (Birkhead and Møller, 1993; Eberhard, 1996). Females can bias paternity by either (1) differential relative uptake or use of sperm from different males (Bishop, 1996; Bishop et al., 1996; Eberhard, 1996) or (2) increasing their reproductive effort after mating with a preferred male (Thornhill, 1983; Wedell, 1996).

A crucial question in sexual selection theory concerns the kinds of male traits that are favored by postmating sexual selection, and in particular whether postmating sexual selection merely reinforces the actions of conventional premating sexual selection (Warner et al., 1995). Certain male traits favored under postmating sexual selection are clearly not under direct premating sexual selection, such as the shape of male intromittent genitalia (Arnqvist, 1998; Eberhard, 1985, 1993) or the chemical composition of male secondary substances in the ejaculate (Chapman et al., 1995; Eberhard, 1996; Eberhard and Cordero, 1995; Rice, 1996; Wilson et al., 1997). Other traits, however, seem to be important in both pre- and postmating sexual selection. This is particularly true for overall size. Male body size is not only the trait most generally favored under premating sexual selection (see Andersson, 1994), it also seems to be generally related to relative paternity success

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Received 29 April 1998; revised 26 October 1998; accepted 21 November 1998.

(e.g., Bissoondath and Wiklund, 1997; LaMunyon and Eisner, 1993, 1994; Lewis and Austad, 1990, 1994; McLain, 1980; Otronen, 1994, 1998; Sakaluk and Eggert, 1996; Simmons and Parker, 1992; Simmons et al., 1996; Ward, 1993; Watson, 1991a,b; Wedell, 1991). There are several reasons that females may benefit from biasing relative paternity in favor of large males because phenotypic and genotypic quality often are positively correlated with body size (see Cordero, 1995; Johnstone, 1995), but there is as yet no evidence of adaptive sperm selection by females (Hosken and Stockley, 1998; Wirtz, 1997). The fact that overall body size, or a trait correlated with body size, is positively related to postinsemination paternity success cannot be taken as evidence for cryptic female choice (cf. LaMunyon and Eisner, 1993; Ward, 1993) because body size can be expected to be positively related to the quantity or quality of transferred sperm and/or accessory substances (Berrigan and Locke, 1991; Parker and Simmons, 1994; Simmons and Parker, 1992). The effects of body size on paternity can thus result from sperm competition (Bissoondath and Wiklund, 1997; Simmons et al., 1996). To disentangle the effects of body size per se from the quantitative effects of sperm numbers, we need studies that independently vary male body size and number of sperm transferred (cf. LaMunyon and Eisner, 1994).

This study represents an attempt to estimate the independent effects of male body size and number of sperm transferred on paternity success in the water strider *Gerris lateralis* (Heteroptera, Gerridae). We achieved this by measuring the effects of male body size and male recovery period on both relative male fertilization success and female reproductive effort subsequent to focal matings, in a factorial experiment with orthogonally crossed factors. Because male recovery period (i.e., time since last copulation) is found to have a strong impact on the number of sperm transferred at each mating, this design allows us to estimate the independent effects of male size and sperm numbers, thus extending previous attempts to do so (cf. Bissoondath and Wiklund, 1997; LaMunyon and Eisner, 1994; Simmons et al., 1996).

METHODS

Study organism

Water striders inhabit water surfaces of various aquatic habitats both as juveniles and adults and are predators/scavengers feeding mainly on arthropods trapped at the water surface (Andersen, 1982; Spence and Andersen, 1994). Female water striders of the genus *Gerris* are highly polyandrous and may mate several times per day. The mating system is characterized by male harassment of females and has been described as convenience polyandry (see Arnqvist, 1997; Rowe et al., 1994, for reviews). In general, there seems to be weak last-male sperm precedence, but large intraspecific variation in paternity success has been documented (Arnqvist, 1988; Arnqvist and Danielsson, 1999; Danielsson, 1999; Rubenstein, 1989). Male *G. lateralis* may mate several times in rapid succession (Arnqvist, 1997), and the relatively small ejaculate consists of little else but sperm (Andersen, 1982). Average copulation duration in *G. lateralis* is 19.5 min (SE = 1.47) (Rowe and Arnqvist, 1996).

Collection and rearing

During May and June 1997, we collected male and female *Gerris lateralis* from populations in Ostnäs and the River Tavleån, both situated in the vicinity of Umeå, Sweden. The experiments were conducted in the laboratory, at 20°C (± 2°), under a simulated natural light regime. Before experiments, females were kept separated from males in large aerated tanks (1 m diam, water depth 12–20 cm). Males were kept with nonexperimental females at a sex ratio of approximately 2:1 in aerated aquaria (25×40 cm, water depth 10–15 cm). Both sexes were fed frozen early instar *Gryllus* crickets ad libitum and were provided with styrofoam pieces as resting sites. The water was changed each week and remaining excess food was removed regularly.

Sterile male technique

We estimated male fertilization success using the sterile male technique originally described by Parker (1970). Males were sterilized by exposure to high-energy X-rays. Males assigned to the irradiation treatment were collected while mating and isolated from females about 1 h before the irradiation treatment, which took place between 1600 h and 1700 h the day before the experimental matings. Males were placed in a petri dish in front of a linear electron accelerator with 6 MV photon beams. A 14-mm thick disc of Plexiglas was placed on top of the dish to prevent the water striders from occupying the dos-buildup area. A water equivalent phantom was placed underneath for backscattering. Males received an absorbed dose of 130±3% Gy with a dose rate of approximately 10 Gy/min. After irradiation, males were kept isolated individually in cups (6 cm diam) with water, food, and Styrofoam pieces. Sperm of irradiated males are able to fertilize eggs but carry lethal mutations that prevent normal embryonic development. The irradiation treatment used here is known to decrease the egg viability rate in this species from the normal 92.2% to 24.9% (see Arnqvist and Danielsson, 1999). In the experiments described below, each virgin female was mated with three males; first with two irradiated males (R1 and R2) and then with a focal normal male (N). The proportion of viable eggs laid by a female subsequent to these matings will hence be proportional to the relative fertilization success of the normal male (*P3*). This proportion will represent a slight overestimate of the true value of last-male fertilization success for each female, but because we dealt exclusively with variance in relative fertilization success across normal males, we used this proportion as our measure of fertilization success (see below).

Male size and recovery period

Before the experiment, we used a caliper (0.02-mm resolution) to make preliminary measures of the body length of all males captured in Tavleån. Two groups, representing the approximate 25% tails of the size distribution, were selected as experimental males (small and large). Postexperimental measures of all individuals, using a digitizing tablet (Summasketch III) under a side-mounted camera lucida attached to a dissecting microscope (Leica MZ8), verified that this preliminary selection had the desired effect: the average body lengths of small and large males were 7.67 (SE = 0.03) and 8.33 (SE = 0.03) mm, respectively ($t = 10.98$, df = 62, $p < .001$; average body size difference 9%). The intermediately sized males from the size selection procedure (mean body length 7.97mm, SE = 0.02 mm) were assigned to the irradiation treatment and used as second mates (R2). Irradiated males mating as first mates (R1) were collected from Ostnäs and were also of intermediate size (mean body length 8.07mm, SE = 0.03 mm). We collected normal males (small and large) from stock aquaria while they were copulating and thereafter isolated them for either 48 h or 2 h before experimental matings. These focal males thus form one group with a long and one with a short recovery period (i.e., time since last copulation). During this premating isolation, males were kept individually in cups (6 cm diam) provided with water, food, and Styrofoam pieces.

Experimental matings

To ensure that only virgin females were used, we checked the fertilization status of individually isolated females before the experiment during a minimum of 4 days. Females laying any fertile eggs during this period were discarded. Each virgin female was mated with two irradiated males (R1 and R2), with an intermating interval of 4–6 h, and with a third normal male (N) on the following day. The focal N males were either small or large, and had either long or short recovery period (see above). Thus, the mating design is a 2×2 factorial design ($N_{tot} = 64$). In all matings, copulation time was measured by spot checks each minute, and copulations that exceeded a maximum duration (2.5 h for R males and 3 h for N males) were carefully interrupted by gently separating the sexes. Copulation time was defined as the duration of the period of genital intromission and hence did not include the postcopulatory noncontact guarding phase (Arnqvist, 1997). Matings were staged in plastic jars (15×20 cm, water depth 6 cm).

After the three matings, females were isolated in the mating jars and provided with one thin piece of Styrofoam (2×1 cm) and one piece of balsa wood (2×1 cm) as oviposition substrates. One frozen cricket (length 0.5–1 cm) and one frozen *Drosophila* fruit fly were added each day. After 4 days, the water was changed and new oviposition substrates were introduced. We collected eggs a second time after another 4 days. The eggs were allowed 8 days of maturation in plastic cups filled with water (20°C), before the number of viable and nonviable eggs were counted (egg age span 8–12 days). Only eggs that showed normal development with red eyespots and legs clearly visible were regarded as viable. Partly developed and opaque eggs were considered nonviable. After 8 days of egg laying, all females were frozen individually in 0.5-ml Eppendorf vials for postexperimental measures of body length.

Control matings

The relationship among ejaculate size, male body size, and recovery period was established by sperm counts derived from a series of control matings. Nonvirgin females were isolated for 2 days before control matings. Each female ($N_{tot} = 36$) was then allowed to mate with a normal male (male treatments as above) in plastic cups (6 cm diam; no water). Copulation duration was recorded by continuous observation. To prevent sperm transport/migration from the bursa copulatrix to the spermatheca, females were frozen individually in Eppendorf vials immediately after the copulation was terminated. Sperm transport/migration is a relatively rapid process in *Gerris* (a matter of a few hours; Andersen, 1982), so any sperm in the bursa can safely be assumed to originate from the last mating.

The female gynatrial complex was subsequently removed using a dissecting microscope and placed in 0.5 ml distilled water. The spermatheca was thereafter removed, and the remaining bursa copulatrix (the gynatrial sac) was ruptured. The water and the bursa were transferred to an Eppendorf vial filled with distilled water to a total volume of 1.5 ml and vortexed for 1 min. We placed five subsamples (each of 50 μl) on a microscope slide and allowed them to dry. We then counted the number of sperm within each subsample directly using a microscope (100×).

We estimated ejaculate volume by first measuring the area of each visible sperm aggregation in the bursa prior to vortexing, by placing a digitizing tablet (Summasketch III) under a side-mounted camera lucida attached to a dissecting microscope (Leica MZ8) (see Arnqvist and Danielsson, 1999). Ejaculate volume was thereafter estimated based on the assumption that the shape of each sperm aggregation could be described by an ellipsoid.

Table 1

Analysis of variance of the number of sperm transferred by males in the control matings

Source	SS	df	MS	*F*	*p*
Male body size	0.255	1	0.255	1.174	.286
Male recovery period	0.905	1	0.905	4.167	.046
Body size × recovery period	0.254	1	0.254	1.173	.286
Error	6.955	32	0.217		

Data analysis

The response variable in studies of relative fertilization success is typically a proportion, but conventional general linear models are nevertheless applied by tradition. Estimates from such analyses may be biased not only as a result of the bounded distribution of the response variable, but more importantly as a consequence of the non-normal and nonconstant binomial variance and the lack of recognition of the sample size on which each proportion is based (Aitkin et al., 1989; Crawley, 1993; McCullagh and Nelder, 1989). To avoid these problems, we chose to estimate the effects of male size, recovery period, and copulation duration on the proportion of eggs fathered by the last male to mate (*P3*) by more appropriate statistical models. We used a generalized linear model of the number of viable eggs per female, using binomial errors with the total number of eggs laid per female as the binomial denominator and a logit link function (Crawley, 1993). To compensate for overdispersion (McCullagh and Nelder, 1989), we implemented the method of Williams (1982) before statistical inference. Generalized linear models were estimated with GLIM, and all other statistical evaluations were performed with SYSTAT.

RESULTS

Control matings

The repeatability of sperm counts across subsamples was high (0.922;($F_{35,144} = 59.33$, $p < .001$) (Lessels and Boag, 1987), confirming that our measure of sperm number reliably estimates the number of sperm contained in a given female's bursa copulatrix. For the analyses below, we thus used the average sperm count in each mating as the dependent variable. A two-way analysis of variance of the number of sperm transferred (log transformed) showed that, as expected, males with a long recovery period transferred almost twice as many sperm in a given mating as did males with a short recovery period (average number±SE of sperm in female bursa, 479.3±81.0 versus 245.7±81.0; Table 1). However, neither body size nor the interaction between body size and recovery period had any detectable impact on number of sperm transferred (Table 1). There were, in contrast, no effects of male size ($F_{1,32} = 1.56$, $p = .221$), recovery period ($F_{1,32} = 2.28$, $p = .141$) or their interaction ($F_{1,32} = 1.99$, $P = .168$) on sperm transfer rate (log number of sperm transferred / copulation duration). Hence, we found no support for a higher sperm transfer rate among large males (cf. Berrigan and Locke, 1991; Parker and Simmons, 1994; Simmons and Parker, 1992) or males with a longer recovery period.

A two-way analysis of variance of copulation duration (log transformed) showed that males with a long recovery period also copulated for twice as long as did males with a short recovery period (28.0±1.2 versus 13.8±1.2 min; $F_{1,32} = 8.98$, $p = .005$), whereas neither body size nor the interaction between the two had any detectable impact on copulation du-

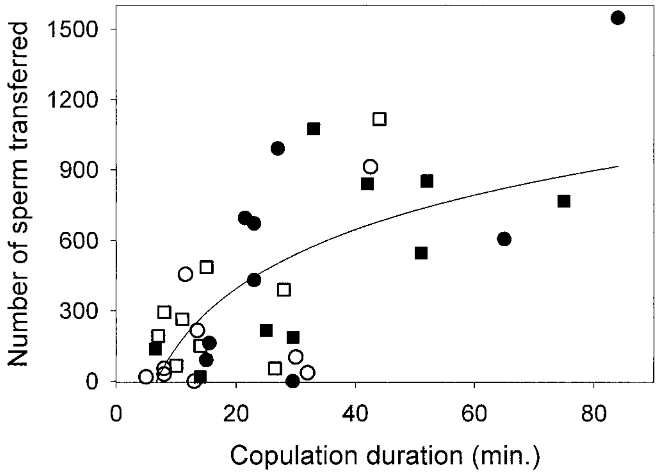

Figure 1
The relationship between number of sperm transferred in a given mating and the duration of copulation for large (circles) and small (squares) males with either short (open symbols) or long (filled symbols) recovery period.

ration ($F_{1,32} = 0.05$, $p = .816$ and $F_{1,32} = 0.00$, $p = .999$, respectively).

In summary, male recovery period had a strong effect on the number of sperm transferred in a given mating, and this effect was a result of differences between males in copulation durations rather than in sperm transfer rates (see also Figure 1). This interpretation was confirmed by introducing copulation duration as a covariate to the analysis of variance presented in Table 1. In this analysis of covariance, copulation duration ($F_{1,31} = 12.44$, $p < .001$) was the only factor significantly affecting the number of sperm transferred ($F_{1,31} < 1.96$, $p > .172$ for all other factors). Analyses identical to the ones of sperm number, but instead performed on ejaculate volume, gave results that were qualitatively identical and quantitatively similar to those presented above.

Experimental matings

Sperm precedence

The estimates of sperm precedence of the last male to mate did not differ during days 1–4 and 5–8 (paired *t* test on arcsine-transformed data, $t = 439$, df = 57, $p = .662$), and the repeatability over the two periods in estimated *P3* was high (arcsine-transformed data, $r = .765$, $p < .001$). Hence, data from days 1–4 and 5–8 were pooled for each female to provide an overall estimate of *P3*. This forms our measure of the relative fertilization success of the last male in all subsequent analyses.

Our factorial variables alone (i.e. male size, male recovery period, and their interaction) did not collectively affect sperm precedence of the last male ($\chi^2 = 3.562$, df = 3, $p = .313$). The copulation duration of males, however, had a highly significant impact on *P3* (log-likelihood ratio test of hierarchical addition of the four mating duration variables, $\chi^2 = 15.461$, df = 4, $p = .004$), primarily due to effects of the copulation duration of the last male (Table 2). The fertilization success of the last male increased with his copulation duration up to durations of about 60 min, but decreased again in greatly extended copulations (Figure 2a). In contrast, the fertilization success of the last male to mate tended to decrease with increasing copulation duration of the female's previous mates (R1 and R2; Figure 2b), though this trend was not significant (Table 2).

Table 2
The result of a generalized linear model, using binomial errors and a logit link function, of the estimated proportion of eggs fathered by the last male to mate (*P3*) (df = 52 in all tests of single factors)

Source	Estimate	SE	*t*	*p*
Last male's body size	−0.276	0.420	0.656	.514
Last male's recovery period	−0.132	0.538	0.246	.807
Last male's body size × last male's recovery period	−0.645	0.426	1.513	.136
Copulation of duration of last male	0.036	0.021	1.705	.094
(Copulation duration of last male)^2	−0.236	0.107	2.209	.032
Avg. copulation duration of previous matings	−0.002	0.013	0.194	.847
(Avg. copulation duration of previous matings)^2	0.007	0.047	0.150	.881

Log-likelihood ratio test of full model: $\chi^2 = 19.022$, df = 7, $p = .008$

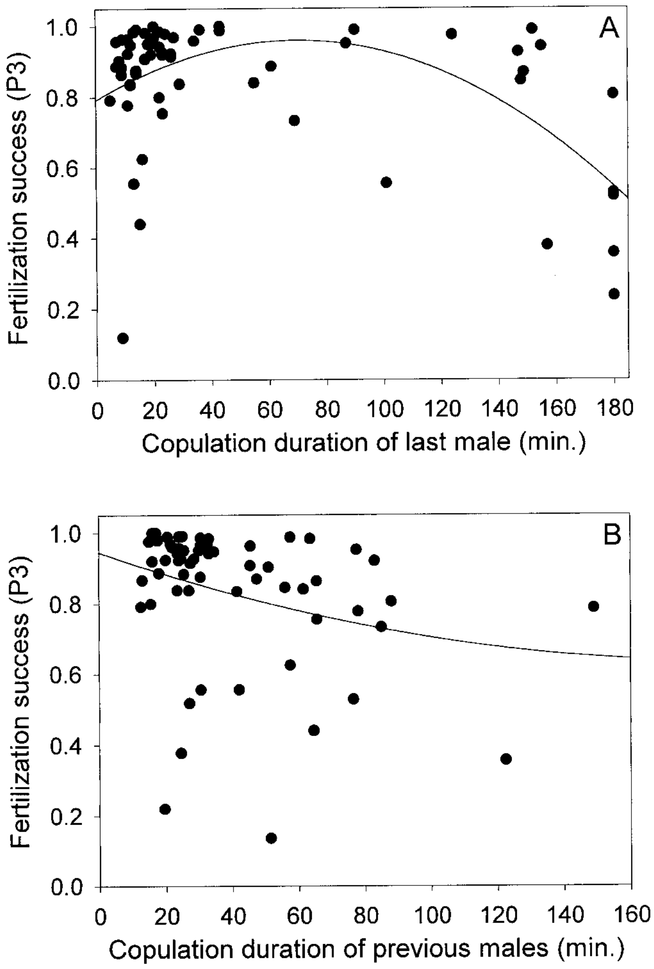

Figure 2
The relationship between the relative fertilization success of the last male to mate with a given female (*P3*) in a triple-mating experiment and (A) the copulation duration of the last male, (B) the average copulation duration of the first and second males (see Table 2).

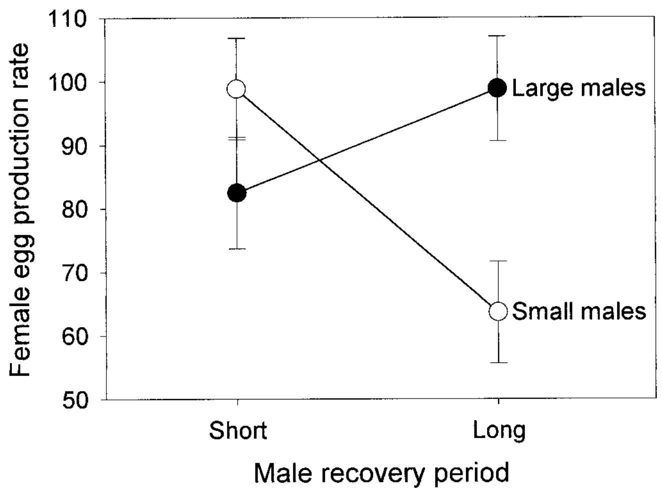

Figure 3
The impact of male recovery period and male body size on female egg production rate (number of eggs laid during eight days) (see Table 3). Error bars represent standard errors.

Table 3
Analysis of covariance of female egg production rate

Source	SS	df	MS	F	p
Last mate's body size	1773.0	1	1773.0	1.724	.195
Last mate's recovery period	1325.7	1	1325.7	1.289	.261
Last mate's body size × last mate's recovery period	7063.1	1	7063.1	6.866	.011
Female body size	851.5	1	851.5	0.828	.367
Last mate's copulation duration	110.5	1	110.5	0.107	.744
Previous mates' copulation duration	253.3	1	253.3	0.246	.622
Sperm precedence of last mate	4912.1	1	4912.1	4.775	.033
Error	57603.4	56	1028.6		

Overall, the intraspecific variance in last-male sperm precedence was strikingly high. The coefficient of variation of arcsine-transformed *P3* values was 38.2%. Though highly significant, our model only explained a relatively small proportion of this variation. The deviance ratio of the model presented in Table 2 $[(D_{\mathrm{null}} - D_{\mathrm{full}})/D_{\mathrm{null}}]$ was 0.367, and the multiple R^2 of the corresponding general linear model on arcsine transformed *P3* values was .350, both indicating that our model accounted for approximately 35% of the variance in last male fertilization success.

The proportion of the observed variance in copulation duration that was due to differences among females (cf. Rubenstein, 1989), as opposed to among males within females, was small but significant (repeatability across females of log-transformed copulation duration = 17.7%, $F_{71,144} = 1.630$, $p = .007$) (Lessels and Boag, 1987). This result is in accordance with earlier findings showing that copulation duration is determined primarily by males in water striders (Arnqvist and Danielsson, 1999; Rowe and Arnqvist, 1996).

Female egg production rate

Female egg production rate was not affected by the last male's size or recovery period (two-way ANOVA; $F_{1,60} < 1.31$, $p > .25$ in both cases). However, the interaction between these two factors had a highly significant impact on egg production rate (two-way ANOVA; $F_{1,60} = 9.728$, $p = .003$). Female egg production rate increased with male recovery period in large males but decreased with male recovery period in small males (Figure 3). A series of sequentially Bonferroni adjusted posthoc tests (Holm, 1979) revealed that this interaction was primarily due to females mated with small males with a long recovery period exhibiting a relatively low egg production rate. These females differed both from those mated with large males with a long recovery period ($t = 3.15$, df = 20, $p = .004$) and those mated with small males with a short recovery period ($t = 3.00$, df = 32, $p = .005$).

To further partition variance in female egg production rate, we also performed an analysis of covariance including four covariates: female body size, copulation duration of last male, average copulation duration of previous mates, and the observed degree of sperm precedence. This analysis generated two insights (see Table 3). First, the interaction effect mentioned above was resistant to the inclusion of the covariates and remained an important determinant of egg production rate. Second, when controlling for copulation duration as well a series of other factors, female egg production rate was positively related to the relative paternity success of the last male to mate (Table 3, Figure 4). In other words, females that mated with males that achieved a relatively high fertilization success produced many eggs during the period after that mating.

DISCUSSION

Our experiments revealed extensive variation in male postmating reproductive success in *Gerris lateralis*. This was due both to differential fertilization success among males and differences in female offspring production rate after the focal matings. Because the patterns detected in our study differ considerably between these two mechanisms of postmating sexual selection, we discuss these topics separately.

Sperm precedence

We failed to find any direct or indirect effects of male size on relative fertilization success. Thus, our results do not lend any

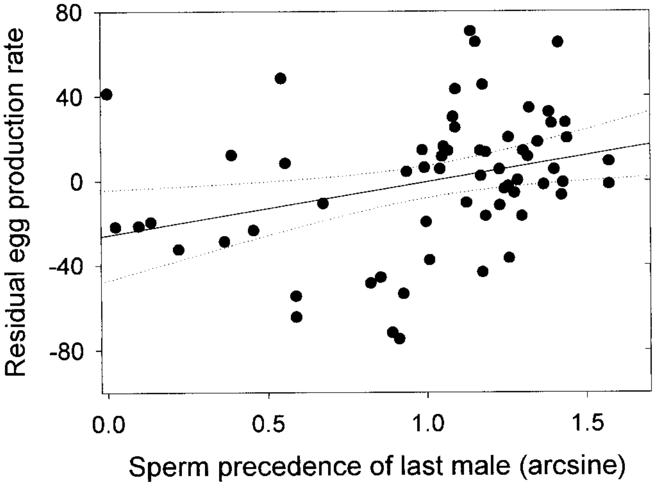

Figure 4
The relationship between the degree of sperm precedence (arcsine-transformed *P3*) and a measure of female reproductive effort. Dotted lines represent 95% CI of the linear regression ($F_{1,63} = 6.46$, $p = .014$). Residual egg production rates were generated in an analysis of covariance, where effects due to male body size, male recovery period, the interaction between these two factors, female body size, and the copulation durations of the last as well as the previous mates were controlled for (see also Table 3).

support to the general suggestion that females preferentially select sperm from large males to fertilize their eggs (Eberhard, 1996; LaMunyon and Eisner, 1993; Simmons et al., 1996; Ward, 1993). On the contrary, the results strongly indicate that numerically based sperm competition is a key factor in determining relative male fertilization success (cf. Parker, 1990). The fact that copulation duration was the only significant determinant of sperm precedence supports this interpretation because the number of sperm transferred in a given mating was directly related to copulation duration. The fact that sperm precedence was positively related to last-male copulation duration in copulations of normal length (see Methods), and at least tended to be negatively related to the copulation duration of previous mates, further supports this scenario. These results are also in accord with those of Rubenstein (1989), who found sperm precedence to be related to the relative copulation duration of the two males in the water strider *Aquarius remigis*.

It is unclear why greatly extended copulations were associated with a lower relative fertilization success, despite the fact that one cwould expect more sperm to have been transferred in these matings. One possibility is that males tend to extend the duration of matings with low sperm transfer rates, due to incorrect genital alignment, for example. Another possibility is that these males were, with limited success, attempting to avoid complete or partial female sperm dumping by prolonging copulations. Though female sperm dumping (i.e., cases where the female discards sperm/ejaculate from the last mating; Eberhard, 1996), has not been studied directly in water striders, behavioral observations (Arnqvist and Danielsson, unpublished) as well as bimodal distributions of sperm precedence (Arnqvist and Danielsson, 1999; Danielsson, 1999) suggest that female sperm dumping may be an important source of variance in male postinsemination success.

Several authors have pointed out that our understanding of the sources of variance in sperm precedence is very limited (e.g., Eberhard, 1996; Lewis and Austad, 1990). A particularly interesting aspect of our results is the relatively low degree of variance in sperm precedence that was collectively accounted for by our experimental variables. Though rarely reported, this seems to be the case in most other studies as well (e.g., Cook et al., 1997; Lewis and Austad, 1990; Otronen, 1997, 1998; Rubenstein, 1989; Simmons et al., 1996). In our case, this is clearly not due to low statistical power because we maximized variance in our factorial variables (used only the largest and smallest males that had experienced either a very short or very long recovery period), controlled for the important impact of copulation duration, and used a large number of replicates. Despite this fact, our statistical models accounted for a minor proportion of the variance in sperm precedence among male *G. lateralis* (35%). A larger part of the variance was apparently due to factors unrelated to male size, recovery period, or copulation duration. Although variance in estimated sperm precedence will certainly be introduced by variance in fertility among irradiated males, the fact that the degree of sperm precedence is repeatable across males in this species (Arnqvist and Danielsson, 1999), as well as in other insects (Lewis and Austad, 1990; Otronen, 1997; Wilson et al., 1997) strongly suggests that random factors alone are not responsible for this residual variation.

A number of phenotypic and/or genotypic characteristics could be important in determining relative fertilization success. For example, Arnqvist and Danielsson (1999) demonstrated that the degree of sperm precedence in this species is affected by the shape of the male's genital sclerites, showing that variation in male genital morphology can determine relative paternity success (Arnqvist, 1998; Eberhard, 1985). Similarly, biochemical characteristics of the ejaculate or the sperm cells themselves are known to affect sperm precedence (see Eberhard, 1996; Eberhard and Cordero, 1995). The success of a given male is also likely to depend in part on the female, generating an interaction between male and female phenotypic and/or genotypic characteristics. Such complex patterns of partial or complete incompatibility between the mates (see Zeh and Zeh, 1996, 1997) has been shown to affect male fertilization success in several species (Arnqvist and Danielsson, 1999; Bishop et al., 1996; Clark and Begun, 1998; Hughes, 1997; Olsson et al., 1996; Wade et al., 1995; Wilson et al., 1997) and are consequential in this context because they suggest that statistical models including only male characteristics may in general be incapable of accounting for large proportions of variance in relative male fertilization success.

Female reproductive effort

Two results strongly suggest that female water striders bias paternity in favor of certain males by modulating the rate of offspring production following copulation with a given male (i.e., cryptic female choice). First, female egg production rate decreased with recovery period in small males, a pattern that was reversed in large males. The fact that females reduced their egg production rate when mated with small males that transferred a large number of sperm implies that females possess mechanisms by which they are able to disfavor small males as fathers of their offspring. This pattern can clearly not be explained by male–male interactions alone. Second, we found a positive relationship between *P3* and female egg production rate, when controlling for female size, copulation durations, and a series of other factors, implying that females invested more in offspring production after copulations with males that were also relatively more successful in terms of fertilization. The most parsimonious explanation for this pattern is that males able to transfer competitively superior ejaculates (e.g., large volume, many sperm, more mobile sperm, large amounts of accessory substances, biochemical characteristics) were not only relatively successful in terms of sperm precedence, but were also better able to stimulate female offspring production (see Eberhard, 1996). Again, this pattern cannot be explained by male–male interactions alone, but the effects must be mediated by female mechanisms that directly or indirectly favor certain males over others.

In insects where male ejaculates contain nutrients that are transferred to the female (i.e., a nuptial gift), such as in certain butterflies and bushcrickets, sperm precedence is known to covary with female reproductive rate (Svärd and McNeil, 1994; Wedell, 1991; Wedell and Arak, 1989). In such cases, however, this may result from a direct relationship between the number of sperm transferred and the amount of nutrients transferred in a given mating because the latter are used by females for egg production. In other species, females apparently increase their offspring production rate either when mated with males with large sexual ornaments or when allowed to freely choose their mate (e.g., Burley, 1988; de Lope and Møller, 1993; Eberhard, 1996; Massa et al., 1996; McLain and Marsh, 1990; Petrie and Williams, 1993; Simmons, 1987; Swaddle, 1996; Thornhill, 1983). However, few studies have reported a positive covariance between male sperm precedence and female offspring production rate in species where no significant paternal investment occurs (cf. Clark et al., 1995; Clark and Begun, 1998). A positive relationship between these sources of variance in male paternity success have important consequences in terms of postmating sexual selection. Successful males will have a twofold advantage: they will not only achieve a high relative fertilization success but will also enjoy a high female offspring production rate. Thus, future studies should seek to identify the female mechanisms, as well as the causal male traits, that are responsible for the pattern documented here.

Sperm depletion and effects on previous estimates of sexual selection

The production of sperm and accessory substances in the ejaculate involve certain costs to males, and limitations on male sperm production rate are manifested as a positive relationship between time since last mating (i.e., the recovery period) and the number of sperm transferred in a given mating in many species (see Dewsbury, 1982; Eberhard, 1996; Møller, 1991; for reviews). Our study showed that male water striders are no exception to this rule. The number of sperm transferred by males increased with the recovery period, and male recovery rate was apparently independent of body size.

Our findings have far-reaching implications for our understanding of sexual selection in these insects. Numerous studies have shown that male mating success is positively related to male body size in water striders and have thus argued that sexual selection favors large males in this group of insects (e.g., Arnqvist, 1992; Arnqvist et al., 1996; Fairbairn and Preziosi, 1994; Preziosi and Fairbairn, 1996; Sih and Krupa, 1992). In light of the results of the current study, it is clear that the relationship between male body size and reproductive success is more complex than previously thought and that mating frequency data alone are insufficient to model male net reproductive fitness. Large size in males may be positively related to mating frequency and female reproductive effort (see above), but these effects will at least in part be offset by limitations in male sperm production rate. Thus, although large males may mate more frequently, small males should copulate for longer, transfer more sperm in each mating, and hence gain higher fertilization success per mating due to average longer recovery periods (see Pitnick, 1991; Ward & Simmons, 1991, for similar results in other insects). A strong indication that this scenario is indeed significant was provided by Rowe and Arnqvist (1996), who found that although large males of three different *Gerris* species mated 15% more frequently, they also copulated for a 16% shorter period than did small males. Hence, pre- and postmating sexual selection may often act antagonistically on male body size, at least in this group of insects. The relative importance of mating success and postmating fertilization success will to some extent depend on the gravity of sperm limitation (i.e., the average male mating frequency in a population—density, reproductive activity, sex ratio), as well as a series of other factors.

We thank Anne Töyrä, Tina Nilsson, Thomas Mårtensson, and Michelle Arnqvist for assistance with the experiments and Nina Wedell for discussions on female reproductive rate. John R. Spence and two anonymous reviewers provided constructive comments on an earlier version of this contribution. This study was made possible by financial support from The Swedish Natural Science Research Council to G.A. and from Rådman och Fru Ernst Collianders stiftelse, Helge Ax:son Johnsons stiftelse, Larsénska fonden, and the Royal Swedish Academy of Sciences to I. D.

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