ANIMAL BEHAVIOUR, 2003, **65**, 851–858
doi:10.1006/anbe.2003.2112,

The role of mating history and male size in determining mating behaviours and sexual conflict in a water strider

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*(Received 10 September 2001; initial acceptance 21 December 2001;
final acceptance 30 July 2002; MS. number: A9160)*

We conducted three experiments to test the effects of mating history of both sexes and of male body size on mating behaviours in the water strider, *Gerris buenoi*. Our manipulations influenced the interests of both sexes and, thus, the degree of conflict over mating behaviours. Mating history was a dichotomous variable (deprived/mated), depending on holding conditions in the laboratory. Experiment 1 considered and found independent effects of male and female mating history on latency to copulation and copulation duration. In experiment 2, we manipulated only female mating history, using unsuccessful struggle rates as evidence for female reluctance and conflict over mating. Finally, we investigated the relation between male body size and mating history on copulation duration. We predicted that intersexual conflict over mating would be lowest when females were deprived, because female interests under these conditions should more closely match those of males. Deprived females began mating in half the time of mated females and were twice as likely to mate because of reduced reluctance. Furthermore, copulation duration for deprived males was about one and a half times longer than that for mated males. Although previous studies examining nonrandom mating patterns by size predicted longer copulations for small males, we found that small males prolonged copulation when deprived more than large males. We conclude that females primarily influence copulation frequency, but males primarily influence copulation duration. Our results favour the hypothesis that reduced mating opportunity for small males accounts for their extended copulation duration. Finally, our findings provide evidence for strong effects of male body size on selection mechanisms in water striders, and support the hypothesis of conflicting pre- and postcopulatory selection mechanisms in this group.

Copulation duration can account for a large component of male fitness. Males that copulate longer may transfer more of their own sperm to females, displace more sperm of past males stored within females and protect females from competing males (reviews in Parker 1970, 1984; Thornhill & Alcock 1983; Eberhard 1996). However, copulation duration varies greatly among individuals, and this variation can thereby be important in sexual selection. Factors that affect copulation duration include local operational sex ratio (e.g. Sillén-Tullberg 1981; McLain 1989; Rowe 1992; Vepsäläinen & Savolainen 1995), presence of competitors (e.g. Parker 1970; Alonso-Pimentel & Papaj 1989; McLain 1989; Siva-Jothy 1989), male phenotype (e.g. size: Ward & Simmons 1991; Parker & Simmons 1994; Rowe & Arnqvist 1996) and female phenotype (e.g. Rowe & Arnqvist 1996; Parker et al. 1999; Bonduriansky 2001; Engqvist & Sauer 2001). Too often it is difficult to disentangle potential underlying causes of patterns. However, in a remarkable series of studies on dung flies, *Scathophaga stercoraria*, each of these potential effects has been isolated (e.g. Ward & Simmons 1991; Parker & Simmons 1994, 2000; Parker et al. 1999). These studies have shown that increased copulation duration by small males may be a means of compensating for reduced copulation frequency in species where large males are favoured in precopulatory choice, for lower sperm transfer rates, or for discrimination against their sperm by females.

Although most studies have focused on males, females may also influence copulation duration. First, the state of the female may affect male optima. For example, males may adjust copulation duration based on the female's stores of sperm from previous males (Parker et al. 1997; Parker 1998; Andres & Rivera 2000), or based on the value of the female to the male (e.g. fecundity: Parker et al. 1999; Bonduriansky 2001; Engqvist & Sauer 2001). Alternatively, females may directly influence copulation duration by actively terminating copulations (reviewed in Eberhard 1996). We may expect such behaviour because

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copulation duration can have important beneficial or detrimental effects on females. For example, increasing copulation duration may increase or decrease predation costs to females (Gwynne 1991; Clutton-Brock & Parker 1995). It is easy to see that, in many cases, sexual conflict will occur over copulation duration where male optima may be higher than those of females.

We focus here on the roles of males and females, and their physiological and behavioural states, in determining copulation durations of the water strider, *Gerris buenoi*. Sexual conflict in water striders has been well studied (reviews in Rowe et al. 1994; Arnqvist 1997). Mating is frequent and costly to females, and females consequently resist mating. The costs of mating include increased predation (Arnqvist 1989; Fairbairn 1993; Rowe 1994) and elevated energy requirements while carrying males (Watson et al. 1998), and each cost will be an increasing function of copulation duration. Copulation duration varies between (Fairbairn 1990; Arnqvist & Rowe 1995; Rowe & Arnqvist 2002) and within species (Rowe 1992; Arnqvist & Rowe 1995; Vepsäläinen & Savolainen 1995; Danielsson 2001). Copulation duration appears to vary with male size and with their perception of mating opportunities, so small males, with fewer mating opportunities, copulate longer (Rowe & Arnqvist 1996; Arnqvist & Danielsson 1999; Danielsson 2001). Mating frequency is lower for small males (Rowe & Arnqvist 1996; Danielsson 2001), because they are less able to overcome female resistance (Ortigosa & Rowe 2002). In those species where sperm transfer rates have been measured, there is no indication that these rates are size dependent, but they are instead a simple function of copulation duration (Arnqvist & Danielsson 1999; Danielsson & Askenmo 1999). Males that have recently copulated tend to copulate for shorter periods (Arnqvist & Danielsson 1999), because of either reduced sperm stores or an elevated perception of mating opportunities.

Studies thus far indicate that males determine the duration of copulation (Rowe 1992; Vepsäläinen & Savolainen 1995), so variance in copulation duration has been attributed to males. However, a female role cannot be ruled out because no independent manipulations of relevant female state (e.g. sperm stores or fecundity) have been conducted. For example, large females copulate longer than small females, and this has been attributed to male choice of more fecund females (Arnqvist & Rowe 1995). However, this may instead be the result of the lower load-carrying costs expected for relatively large females (Watson et al. 1998). No studies have investigated the relation between sperm stores and copulation duration in water striders. Independent manipulation of the interests of the two sexes can also enable an evaluation of the role of sexual conflict in determining mating behaviours (Rowe 1992; Vepsäläinen & Savolainen 1995; Lauer 1996; Rowe et al. 1996).

We report on a series of studies aimed at determining the effect of mating history of both sexes and of body size of males on copulation duration in *G. buenoi*. Our study also provided the opportunity to manipulate the degree of conflict between the sexes, and assess its influence on copulation duration and sexual selection. For example, we predicted a high degree of conflict over copulation duration when females had been recently mated and had no need for more sperm, and when males had recently been deprived of mating. Conversely, we predicted that conflict should be reduced when females had been deprived of sperm, but males had recently mated. Finally, our experiments incidentally yielded data on the influence of these variables in determining latency to copulation.

METHODS

Water striders used in all experiments were short-winged individuals collected from a wild population in the Holland Marsh Canal located about 60 km north of Toronto, Ontario, Canada. In the laboratory, sexes were separated and kept in groups of about 20 individuals within large bins (40 × 60 × 8 cm) filled with about 4 cm of dechlorinated water. Each bin was aerated and contained two floating styrofoam strips (3 × 10 cm) for resting and oviposition. Ambient temperature was 20°C and the photoperiod simulated natural conditions. Water striders were fed daily ad libitum freshly frozen fruit flies, *Drosophila melanogaster*, and locusts, *Locusta migratoria*.

Mated (M) and deprived (D) mating treatments were established as follows. The day before beginning an experiment, a subset of insects was removed from their holding bins and paired separately in observation arenas (buckets with a water surface area of 340 cm^2 and a water depth of about 10 cm). Each pair was observed until copulation occurred before being transferred into high-density ‘mixed-sex’ holding bins where the operational sex ratio approximated 1:1 and additional matings were expected to occur. These individuals had, therefore, mated at least once in the 24 h before an experiment and were designated as the recently mated treatment group (M). The remaining individuals continued in their original ‘same-sex’ holding bins and were designated as the deprived treatment group (D).

On the day of each experiment, we placed individual females (from either M or D backgrounds) into replicate arenas 1 h before beginning observations, so that they could acclimate. At this time, females in arenas and males in holding bins received six frozen fruit flies each. All food was removed before introducing a single male into each arena and beginning observations. Each replicate pair was observed at least every 2 min and usually more often for the duration of the experiment.

All statistical analyses were performed using SYSTAT 5.1 (Wilkinson 1988). We performed one- and two-way analyses of variance (ANOVAs) on continuous dependent variables. Variables measuring time were transformed using the natural logarithm to reduce heteroscedasticity and meet statistical assumptions (Hartley’s test). In all experiments, latency and copulation duration are reported in minutes, and only male genital insertions lasting longer than 3 min were included as a copulation event (see also Weigensberg & Fairbairn 1996). Latency to copulation data included the maximum observation time for replicates that did not mate and therefore represent a conservative estimate of mean latency to copulation in each group. Log-likelihood ratios were used to test for treatment effects on frequency data.

Experiment 1: Effect of Mating History in Both Sexes

The first experiment was designed to determine the effects of mating history of both sexes on the time to copulation (latency) and the duration of copulation. Males and females were collected (8–10 June 1998) and separated into 'same-sex' holding bins for approximately 25 days before experimental trials. As with other water strider species (Kaitala 1987; Arnqvist 1988, 1989; Rubenstein 1989), females of this species become depleted of sperm after about 10–12 days in the absence of males (unpublished data).

The experiment consisted of four treatments in a 2 × 2 factorial design: (1) mated female and mated male (M_fM_m, $N=18$); (2) deprived female and deprived male (D_fD_m, $N=15$); (3) deprived female and mated male (D_fM_m, $N=19$) and; (4) mated female and deprived male (M_fD_m, $N=17$). For each replicate pair, we recorded latency to copulation and duration of copulation. Replicates were observed continuously until the end of copulation or for a maximum of 330 min.

Experiment 2: Female Mating History, Latency and Reluctance

In this experiment, we measured the effect of female mating history on female reluctance behaviour to determine whether variation in latency, observed in experiment 1, was attributable to male or female behaviour. Experimental water striders were collected on 10 and 13 July 1998. In the laboratory, males were maintained in mixed-sex holding bins with nonexperimental females at a sex ratio of approximately 1:1 and experimental females (M and D) were kept separate from males in same-sex holding bins for 10–13 days.

In addition to latency and the duration of copulation, we compared female reluctance behaviour between mated females (M, $N=19$) and deprived females (D, $N=16$) by observing harassment rates. We recorded male harassment rate by counting the number of lunges, chases and struggles prior to mating. We also compared male effort in these struggles by comparing the mean duration (s) of those struggles that did not lead to mating (unsuccessful struggles). Replicates were observed continuously until the end of copulation or for a maximum of 167 min.

Experiment 3: Mating History, Male Body Size and Copulation Duration

In this final experiment, we determined the effect of male body size and mating history on copulation duration. Water striders were collected between 16–18 June 1999 and maintained separately by sex in holding bins in the laboratory. Mated and deprived mating treatments for experimental males were established as in experiment 1 and deprived females were kept in same-sex holding bins. Deprived males and all females were held in separate sex bins for 10–12 days before the experiment. All experimental females were deprived of mates to ensure that females were receptive to mating to give small and large males a balanced probability of mating (Ortigosa & Rowe 2002).

We classified males into small and large size classes using the following qualitative approach. First, we divided all males into two groups representing large and small individuals. Large and small individuals within these two groups were divided further in the same manner, yielding a total of four size classes. Males in the extreme large and small groups were individually marked using gold and silver permanent ink and used in these experiments. At the end of each trial, we preserved pairs in 95% ethanol and obtained quantitative body size data using digitizing software. We recorded two replicate measurements for each individual from the tip of the head to the last nongenital segment and calculated mean body size for large (L) and small (S) males. Our subjective allocation of males into size classes successfully distinguished a small and large size class. Mean body size of large males was significantly greater than small males (one-tailed t test: $t_{108}=6.98$, $P<0.0001$).

Thus, the experiment consisted of four mating treatments in a 2 × 2 factorial design: (1) mated large (ML, $N=27$); (2) mated small (MS, $N=27$); (3) deprived large (DL, $N=29$) and; (4) deprived small (DS, $N=28$). We measured latency and copulation duration for each replicate. Trials were conducted over two consecutive days and observations for each trial proceeded until the end of copulation or for a total of 180 min.

RESULTS

Experiment 1

Following 330 min of observation, all but 11 pairs (5 M_fM_m, 2 D_fD_m, 4 D_fM_m) successfully mated at least once. There was no significant difference between treatments in the number of pairs that mated (chi-square test: $\chi^2_3=6.70$, $P=0.082$). However, the mean ($\pm$ SE) latency for mated females (13.8 ± 1.3, $N=35$) was significantly greater than that for deprived females (6.8 ± 1.3 min, $N=34$) (ANOVA: $F_{1,65}=6.98$, $P=0.01$). Mean ($\pm$ SE) latency for mated males (12.3 ± 1.3 min, $N=37$) was greater than for deprived males (7.7 ± 1.3 min, $N=32$), but this difference was not significant ($F_{1,65}=3.13$, $P=0.08$). There was also no significant effect of the interaction between female and male mating history on latency to copulation ($F_{1,65}=0.02$, $P=0.89$; Fig. 1a).

Deprived males copulated significantly longer than did recently mated males (19.0 ± 1.2, $N=26$ and 12.2 ± 1.2 min, $N=30$ respectively; $F_{1,52}=5.31$, $P=0.02$). Mean copulation durations for mated and deprived females were 16.9 ± 1.2 ($N=26$) and 13.6 ± 1.2 min ($N=30$), respectively. There was no significant effect of female mating history ($F_{1,52}=1.26$, $P=0.27$) and no interaction between main effects on copulation duration ($F_{1,52}=0.70$, $P=0.41$; Fig. 1b).

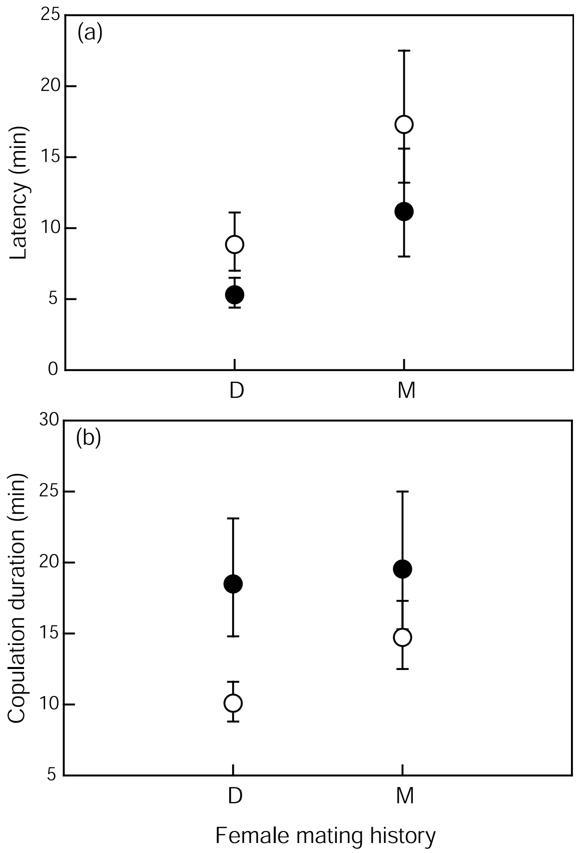

Figure 1. Mean (±SE) effect of male and female mating history on (a) latency and (b) copulation duration (experiment 1). M: Mated; D: deprived. ○: M male; ●: D male. Pairs that failed to mate were scored to have the maximum latency (330 min).

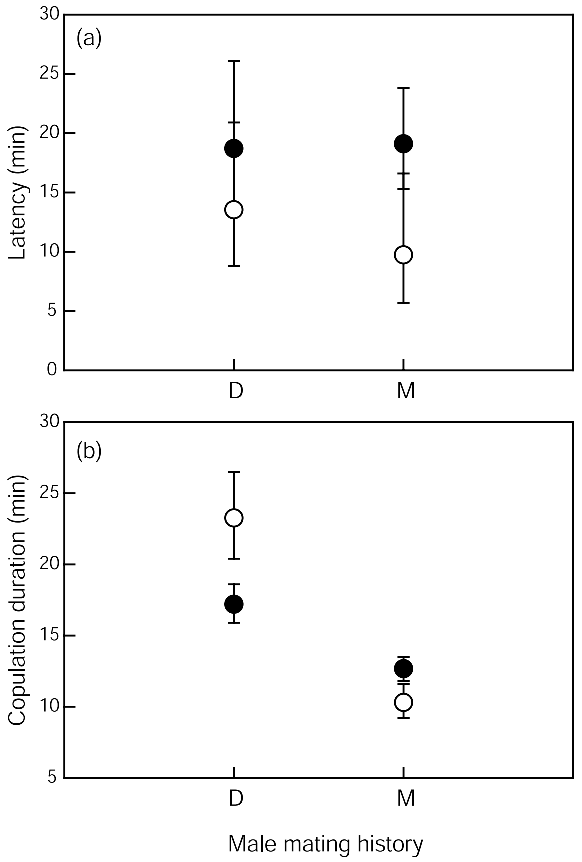

Figure 2. Mean (±SE) effect of male mating history and of male body size on (a) latency and (b) copulation duration (experiment 3). M: Mated; D: deprived. ○: Small male; ●: large male. Pairs that failed to mate were scored to have the maximum latency (180 min).

Experiment 2

Following 167 min of observation, 15 of 16 deprived females paired, but only five of 19 mated females paired. The difference between these groups was significant (chi-square test: χ^2_1=15.93, P<0.0001). The pattern of latency and copulation duration supported results reported in experiment 1. Mean (± SE) latency for mated females (61 ± 1.4 min, N=19) was more than quadruple that for deprived females (12.7 ± 1.4 min, N=16) resulting in a significant female mating history effect (ANOVA: $F_{1,33}$=11.88, P=0.002). Copulation durations in both treatments (M: 9.94 ± 1.3 min, N=5; D: 9.47 ± 1.2 min, N=15) were not significantly different ($F_{1,18}$=0.01, P=0.87).

Of the 16 females in the deprived treatment, 11 mated on their first encounter with a male without resistance, but all 19 females in the mated treatment struggled repeatedly, representing significantly different behaviour between female treatments (chi-square test: χ^2_1=11.67, P=0.001). Therefore, the high frequency and short latency to copulation of deprived females originated from a lack of resistance to male mating attempts, especially considering that males did not significantly vary their effort (unsuccessful struggle duration) towards mate-deprived females (M: 7.26 ± 1.3 s, N=17; D: 8.00 ± 1.7 s, N=5; ANOVA: $F_{1,20}$=0.03, P=0.86).

Experiment 3

Following 180 min of observation time, most pairs (89–96%) had mated, and there were no significant effects of male size or mating history on this component of mating behaviour (chi-square test: χ^2_3=1.74, P=0.628). As in experiment 1, latency to copulation was not affected by male mating history (ANOVA: $F_{1,107}$=0.15, P=0.70; Fig 2a). Mated males had a mean (± SE) latency period of 13.6 ± 1.4 min (N=54), and latency for deprived males was 15.9 ± 1.5 min (N=57). Male body size and the interaction between size and mating history had no effect on latency ($F_{1,107}$=1.58, P=0.21 and $F_{1,107}$=0.20, P=0.66, respectively). The mean latency period for large males was 18.9 ± 1.5 min (N=56) and that for small males was 11.5 ± 1.5 min (N=55).

The effect of male mating history and body size on copulation duration was complex (Fig. 2b). The main effect of male mating history on copulation duration was significant ($F_{1,100}$=30.70, P<0.001), but the effect of male body size was not ($F_{1,100}$=0.22, P=0.64). However, there was a strong significant interaction between male mating history and body size ($F_{1,100}$=6.28, P=0.01). The interaction resulted from a much stronger effect of mating history on copulation duration in small males than that in large males (Fig. 2b). Mean copulation duration in mate-deprived small males was 23.3 ± 1.1 min (*N*=26), 225% longer than recently mated small males whose mean copulation duration was 10.3 ± 1.1 min (*N*=24). The same comparison for large males revealed only a 36% difference in mean copulation duration between deprived and mated males (17.2 ± 1.1 min, *N*=28 and 12.6 ± 1.1 min, *N*=26, respectively).

DISCUSSION

Our results show that male size and the mating history of both sexes independently affected mating behaviours in the water strider, *G. buenoi*. Females appeared to determine when mating occurred, depending in part on the time since their last mating. Once mating took place, the duration of copulation decreased in relation to time since the male's last copulation, and the extent to which a male prolonged copulation was affected by his body size. We now discuss the causes of each result and their implications for sexual selection and conflict in this group.

Female Mating History

Female mating history had a strong effect on latency to mating. Deprived females were more likely to mate (experiment 2), and mated more quickly than did recently mated females in both experiments where female deprivation was manipulated. Differences between experimental protocols (e.g. a two-fold difference in female deprivation period and lack of a mate-deprived male group in experiment 2) may account for the variation in latencies between experiments. The significant effects of mating history on latency appear to be mediated solely by female behaviour. All matings by deprived females occurred because females did not respond with a struggle to male mating attempts. The lack of resistance by sperm-deprived females was clearly adaptive, and parallels those results reported earlier for *Aquarius remigis* (Lauer 1996). In the absence of sperm depletion, females that have been exposed to little male harassment (as were our mated females) are typically more rather than less resistant to mating (Vepsäläinen & Savolainen 1995). Thus, our results demonstrate that sperm depletion acts independently of mating and operational sex ratio history on female resistance.

Female mating history had no effect on the copulation duration in either experiment 1 or 2 (Fig. 1b). This was a surprising result, because females that had been deprived of males were essentially virgins. The lack of sperm in the female should indicate decreased sperm competition, where the potential gain rate of fertilizations is greater, and we would hence expect less time investment by males (Parker et al. 1993, 1997). The idea that copulation duration of a male depends upon the value of his mate is common to a variety of taxa (reviewed in Parker et al. 1997; Elgar 1998; Parker 1998; Bonduriansky 2001). Our result suggests that, during the copulatory phase, either male *G. buenoi* are unable to distinguish females carrying sperm from those that do not, or fertilization gain rate is independent of the amount of sperm present from a prior male. The latter has not been investigated directly (but see Arnqvist & Dannielsson 1999). This lack of discrimination of female mating history by males during copulation contrasts with results from other species (e.g. Suter 1990; Lewis & Iannini 1995), but matches those found in at least one other well-studied species, the dung fly (Parker et al. 1993).

There was no indication that males made a greater effort to mate with sperm-deprived females. The duration of those struggles where females successfully repelled males were independent of female mating history. Thus, males appeared to be unable to discriminate between mated and sperm-depleted females during the precopulatory phase as well as the copulatory phase. Again, this result contrasts with those from other species (e.g. Lorch et al. 1993; Andres & Rivera 2000).

Male Mating History

There were strong effects of male mating history on copulation duration (Figs 1b, 2b), which appeared to result from the males' altered perception of mating opportunities. Mate-deprived males were held in all-male cultures for at least 10 days immediately before the experiments, and were therefore expected to perceive a high search time for additional females. In contrast, mated males were held in mixed-sex cultures for the 24 h before the experiment and mated at least once during this period. These males should have had a perception of much lower mate search times. Increasing search times are expected to lead to increased copulation duration (Parker & Stuart 1976), and our results fit this prediction. This effect has been shown in many species. Our results suggest that male water striders can similarly assess mating opportunities and adjust their copulation duration accordingly. In experiments on the effect of past operational sex ratio, Vepsäläinen & Savolainen (1995) likewise argued that water striders adjust mating behaviours based on information gained in the past.

An alternative hypothesis for our results is that males that had mated in the past 24 h reduced copulation duration because of their own depleted sperm stores. This hypothesis has been advanced for similar mating history effects in related species (Arnqvist & Danielsson 1999; Danielsson 2001), although Arnqvist & Danielsson did not consider the mating opportunity hypothesis that we favour. The sperm depletion hypothesis would be viable if males ran out of sperm before the experiment, or had a reduced supply or transferred sperm at a lower rate. However, neither possibility is currently supported. In the one set of relevant data, male sperm transfer rate of *G. lateralis* (Arnqvist & Danielsson 1999) and fertilization rate of *G. lacustris* (Danielsson 2001) were unaffected by recent mating history.

Male Size

We found strong effects of male size on copulation duration in deprived males. Small males, when mate deprived, more than doubled their copulation durations, but durations for large males increased only by about one-third. We attribute this effect to the size dependence of copulation duration rather than to any difference between size classes in the perception of mating opportunities gained during our treatments. Because small males are poor at overcoming female resistance (Ortigosa & Rowe 2002), and resistance is common (Rowe 1992), we expect small males to have generally reduced mating opportunities (Arnqvist et al. 1996; Rowe & Arnqvist 1996). Resulting increases in mate searching times are expected to lead to the observed increases in copulation duration (e.g. Parker & Stuart 1976; Parker & Simmons 1994). The link between female resistance and male size advantage offers an explanation for our puzzling result that copulation durations were only size dependent in the deprived treatment. Our mated treatment was meant to create a perception of frequent mating opportunities, with little female resistance. We used high-density holding conditions that are known to reduce female resistance (Arnqvist 1992), and allowed all individuals to mate at least once during this period. Thus, males of both size classes experienced recent conditions of relatively high mating frequency and low female resistance. Under these conditions, mating opportunities are expected to be high and equivalent for both size classes. Consequently, copulation durations were short and equivalent between small and large males.

There are two alternative hypotheses for the long copulation durations of small males observed in the deprived treatment. First, small males may have reduced sperm transfer rates, which are expected to lead to longer copulation durations (Parker & Simmons 1994, 2000). However, sperm transfer rates are known to be independent of size in related species (Arnqvist & Danielsson 1999; Danielsson 2001). Moreover, any effect of sperm transfer rate should have also manifested itself in longer copulation durations of small males in the mated treatment, but did not. Second, experience in the wild, before collection, may have resulted in size-dependent perceptions of mating opportunities (mate search times). Although small males may have gained different perceptions of mating opportunities in the wild, it seems highly unlikely that they would retain these over the 10–12-day pre-experimental mate deprivation period. Males of this species adjust their mating behaviours to local conditions within a few hours of exposure (Rowe 1992). Similarly, small males in the mated treatment may have experienced mating opportunities different from those of large males within 24 h of the experiment, but small and large mated males actually did not differ in copulation duration. Finally, it is unlikely that small and large males gained any different perception of mating opportunities during the experiment, because females were unlikely to discriminate in our experiment. Small males are discriminated against only when females are resistant (Ortigosa & Rowe 2002) and we used sperm-depleted females, which have much reduced resistance.

We conclude that copulation duration is both male-size-dependent and sensitive to the perception of male mating opportunities. Although longer copulations of small males appear to be common in *Gerris* (Arnqvist & Rowe 1995; Arnqvist & Danielsson 1999; Danielsson 2001), few studies have examined the cause of this size dependence. In an experiment that shared some similarity with ours, Arnqvist & Danielsson (1999) found no evidence of size-dependent copulation durations in a related species. The reason for this difference is not clear. One possibility is that their sample size (about one-third of ours) was too small to detect a difference. Another is that their mate deprivation period was short, about one-fifth as long as ours.

Sexual Conflict and Sexual Selection

Our results have important implications for sexual conflict and sexual selection in *G. buenoi*. Our experimental treatments can be interpreted as independent adjustments to the interests of males and females in mating behaviours, and thereby the degree of conflict over these behaviours. The source of conflict over both frequency and duration of copulation in this group are the well-known costs of mating to females (Fairbairn 1993; Rowe 1994; Watson et al. 1998). Results from these manipulations, then, yield insights into which sex has the primary influence over the components of mating.

Our results suggest that females have primary influence over copulation frequency, and males have primary influence over copulation duration. Sperm depletion of females should lead to higher mating rates to gain sperm. If females can influence mating frequency, then frequency should increase, and it did in our experiments. Alternatively, mate-deprived males should have, if anything, a higher optimal mating rate, but there was no evidence that they could translate this into a higher success rate of mating attempts. Similarly, virgin females should be of greater value to males, but there was no evidence that males could detect the mating status of females during the precopulatory phase. The primary role of females in determining the outcome of male mating attempts, indicated here, is in agreement with other studies of *G. buenoi* (Rowe 1992; Ortigosa & Rowe 2002) and related species (Arnqvist 1992; Weigensberg & Fairbairn 1994; Vepsäläinen & Savolainen 1995). In contrast, copulation duration appears to be sensitive to the interests of males, but not females. The effects that we found of male size and mating history on copulation durations reflect male interests. Males that had prolonged mate search times, either because of female discrimination or because females are locally rare, extended copulation duration. There was no evidence that females actively influenced copulation duration. Neither sperm-deprived females, nor those copulating with smaller and therefore less energetically costly males (Watson et al. 1998) reduced copulation durations.

Finally, our results confirm the hypothesis that pre- and postcopulatory size advantages conflict in this species (Rowe & Arnqvist 1996; Danielsson 2001). Field surveys have shown that large males have a mating advantage in this and related species, but that it is highly variable over space and time (Arnqvist et al. 1996). Laboratory studies have revealed that there is a large-male advantage in mating frequency and guarding duration, but a small-male advantage in copulation duration (Rowe & Arnqvist 1996). Our results offer an explanation that may account for some of the high variability in mating advantage observed in the field. We have shown that extended copulation duration by small males depends upon past mating opportunities. Therefore, one would expect the overall pattern of large-male mating advantage to be sensitive to local mating opportunities.

Acknowledgments

We wish to thank J. Andres, G. Arnqvist, R. Baker, D. Gwynne, D. Jackson and K. Westlake for advice and comments on earlier versions of the manuscript. Thanks to Y. Cheng and M. Tseng for help in collecting the data. This research was supported with an NSERC Canada research grant to L.R., and A.O. was supported by University of Toronto Fellowships.

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