ANIMAL BEHAVIOUR, 2002, **64**, 369–375
doi:10.1006/anbe.2002.3065, available online at http://www.idealibrary.com on IDEAL®

The effect of hunger on mating behaviour and sexual selection for male body size in *Gerris buenoi*

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(Received 30 April 2001; initial acceptance 25 August 2001;
final acceptance 18 January 2002; MS. number: A9053)

The set of mating behaviours expressed by an individual may depend upon the state of that individual and local environmental conditions. Understanding how these factors affect mating behaviours may elucidate how a mating system operates, and its consequences for the form and strength of sexual selection. We conducted two experiments on the water strider *Gerris buenoi* to (1) determine the effect of hunger on the mating behaviour of both sexes and (2) examine female choice for large males. In our first experiment, we manipulated hunger (20 h starvation) in both sexes and recorded mating, male harassment, copulation duration and guarding duration. We predicted that hunger would increase female reluctance to mate because mating conflicts with foraging. Female hunger (20 h starvation) decreased mating rate by two-thirds but had no significant effect on male mating behaviour. In a second experiment, we examined the effect of female hunger, and resulting reluctance, on sexual selection for large male size. Hungry females (5 h starvation) were placed with two fed males (one large, one small) and we recorded male premating and mating behaviours. We observed significant large-male mating advantage when females were hungry, but not when satiated. Mating efforts (harassment, premating struggles) were similar for both male phenotypes in both female hunger treatments, suggesting that the mating advantage of large males resulted from increased reluctance of hungry females to mate. Neither male body size nor female hunger explained a significant amount of variation in copulation duration or guarding duration. We discuss our results in light of two competing hypotheses for female choice (active and passive) on male body size and suggest that passive choice for large males acts in this system.

Ecological conditions (e.g. population density, predation rate, food availability, operational sex ratio) often shape the behaviour of individuals and constrain the set of behaviours expressed by those individuals. The idea that individuals cannot optimize all behaviours simultaneously has received much attention in behavioural ecology over the last few decades (reviewed Sih 1987; Lima & Dill 1990). A few of these studies have focused specifically on variation in mating behaviour in response to variation in conflicting demands (Partridge & Endler 1987; Sih 1988; Lima & Dill 1990; Sih et al. 1990; Magnhagen 1991; Travers & Sih 1991; Rowe 1992). Surprisingly, studies extending the analysis of behavioural conflicts to sexual selection are relatively scarce in the literature (e.g. Ryan 1985; Endler 1987; Sih & Krupa 1992), even though such conflicts may be central forces shaping mating systems (Emlen & Oring 1977; Crowley et al. 1991).

In some species of water striders, a conflict for females between mating and feeding appears to affect the degree of intersexual conflict over the timing, duration and frequency of mating (reviews in Rowe et al. 1994; Arnqvist 1997). For example, in *Gerris buenoi,* mating conflicts with foraging, and as expected, females mate less frequently when hungry (Rowe 1992, 1994). Decreases in mating rate of hungry females probably results from increased resistance (struggling: somersaults, flips, etc.) by females to repeated male mating attempts, however, this has not been examined. Females usually succeed in rejecting harassing males and, the greater their resistance, the lower the male mating success (Rowe 1992). Consequently, any variation in female resistance can play a dominant role in variation in mating rates of this and many other water strider species (Rowe et al. 1994; Arnqvist 1997).

Female resistance also plays a central role in determining the form and strength of sexual selection on males (reviewed in Rowe et al. 1994; Arnqvist 1997). When female resistance to mating is high, sexual selection on

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0003–3472/02/$35.00/0

male traits is also high. For example, several morphological features in males are favoured by female resistance (Arnqvist 1989; Weigensberg & Fairbairn 1996; Westlake et al. 2000). A similar pattern has been observed in other groups, including seaweed flies (Crean & Gilburn 1998) and dung flies (Blankenhorn et al. 1999), and may be quite widespread given the high frequency of mating systems that include active resistance to persistent male mating attempts (Clutton-Brock & Parker 1995). Those local ecological conditions that affect hunger level in females should alter optimal mating rate in females and therefore the degree of conflict over mating rate between the sexes and the pattern of sexual selection in water striders, and other groups with similar mating systems (Rowe et al. 1994; Arnqvist 1997; also see Arnqvist & Nilsson 2000).

Sexual selection has been reported for a variety of male traits in water striders (reviewed in Arnqvist 1997), but here we focus exclusively on selection for male body size. Convincing evidence of sexual selection for large males exists in several water strider species, including *G. buenoi* (e.g. Fairbairn 1988; Arnqvist et al. 1996; Rowe & Arnqvist 1996). However, there is a good deal of variation within and among species in the intensity of selection on size (Fairbairn 1988; Arnqvist et al. 1996), and this may result from variation in local ecological conditions (Sih & Krupa 1992; Arnqvist et al. 1996; Rowe & Arnqvist 1996). There have been no studies that explicitly consider the effects of individual state (e.g. hunger) on the pattern of sexual selection.

Although it is clear that resistance plays a key role in determining the presence and strength of sexual selection for male size, there are two alternative hypotheses for the mechanism of preference. The first proposes that females resist less with large males. This may occur simply because the energetic costs of these struggles are an increasing function of male size (Watson et al. 1998). Similarly, females may resist large males less if size indicates good genes. In both cases this could be referred to as active choice because the female behaviour (resistance) that results in preference depends upon male phenotype. The alternative hypothesis states that female behaviour is independent of male phenotype and can therefore be referred to as passive choice (Parker 1983; or 'indirect choice' sensu Wiley & Poston 1996). Large males would be favoured simply because they are better able to overcome female resistance. The two hypotheses make different predictions regarding the relationship between mean female resistance and the strength of sexual selection on males. Under passive choice, ecological conditions or female states that lead to low levels of mean female resistance would result in low levels of sexual selection for size compared with conditions or states that lead to high resistance. Under active choice, females will reduce their resistance when presented with large males. There is no reason to expect any change in the relative success of large males as the mean level of female resistance increases.

A straightforward test to distinguish the active and passive hypotheses would include measures of the dependence of female resistance on male size, focusing directly on the mechanism (see Sullivan 1989). The evidence on this point is mixed. Weigensberg & Fairbairn (1996) reported that struggle durations were shorter when water strider females (*Aquarius remigis*) were paired with large males than with small. These data are consistent with active choice, however, no large-male advantage in mating frequency actually occurred in the experiment. In contrast, Crean & Gilburn (1998) report increased struggle durations for large males in a seaweed fly, and that mating success in males was an increasing function of struggle durations.

In this paper, we report on two experiments designed to elucidate the links between female state, mating rate and sexual selection on male size. In the first experiment, we manipulate male and female hunger states independently, and measure resulting mating behaviour. In the second experiment, we manipulate only female hunger and measure its effect on mating success of large and small males, and on premating struggle durations. We use these latter data to distinguish the mechanism of the preference.

METHODS

Gerris buenoi is a relatively small and dimorphic species that expresses an intermediate level of large-male mating advantage (Arnqvist et al. 1996; Rowe & Arnqvist 1996). Mating conficts with foraging in this species, and therefore, hungry females are expected to alter their behaviour when hungry (Rowe 1992, 1994). Females probably face this conflict often, because harassment by males is frequent (up to 47 harassment events/h, Rowe 1992), and females spend a large proportion of their day foraging (about 25%, Rowe 1994) because food often limits egg production rate (Rowe 1993). Frequent food limitation of egg production and the high proportion of time females spend foraging suggests that females are often hungry. Mating in this species appears to be disentangled from oviposition, because females store sperm, and most matings end without oviposition (Rowe 1992). Nevertheless, last-male sperm precedence occurs in the group (Arnqvist 1997), and therefore, high mating rates by males will be favoured by sexual selection.

Short-winged *G. buenoi* were collected from a wild population in the Holland Marsh Canal located about 60 km north of Toronto, Canada in July 1998 and 2000. Individuals were acclimatized in the laboratory in large aerated holding bins (40 × 60 × 10 cm) filled with approximately 4 cm of dechlorinated water. Water striders were provided with floating styrofoam strips (3 × 10 cm) for resting and oviposition and were fed freshly frozen fruit flies (*Drosophila melanogaster*) ad libitum. Ambient temperature was constant at 20 °C and the photoperiod simulated natural conditions. The sexes were held together in these conditions for at least 48 h before applying experimental conditions.

All experimental individuals were fed in holding bins at time zero (t=0 h) to control time since last feeding across all experimental individuals. Food was removed after 1.5 h and, individuals in the nonfed treatment were then deprived of food for the duration of the experiment. Starvation period and duration of experimental observation varied between the two experiments, but in both cases, experimental individuals in the fed treatment were supplied with four freshly frozen fruit flies 1 h prior to beginning observations. At this time, we placed a single female from fed and nonfed treatments into mating arenas (5-litre, round, polypropylene pails filled with approximately 10 cm water). Immediately before commencing observations, we removed all food from the experimental arenas and introduced males.

Experiment 1: Hunger in Both Sexes

Experimental trials were conducted over two consecutive days in July 1998. Nonfed males and females were starved for a 20-h period. The experiment consisted of four treatments following a two-by-two fully factorial design (sex by hunger): (1) fed female, fed male (Fed$_{♀}$Fed$_{♂}$) (*N*=25), (2) fed female, nonfed male (Fed$_{♀}$Nonfed$_{♂}$) (*N*=24), (3) nonfed female, fed male (Nonfed$_{♀}$Fed$_{♂}$) (*N*=25) and (4) nonfed female, nonfed male (Nonfed$_{♀}$Nonfed$_{♂}$) (*N*=25).

We recorded male harassment rate, copulation duration and guarding duration in all treatment replicates. Harassment rate (lunges, chases, struggles) was calculated for the period prior to mating. Mating arenas were observed until termination of copulation or for a maximum of 5 h. Treatments were distributed evenly among two observers and scan samplings of each arena occurred approximately every 20 s. We cannot rule out the possibility that we missed harassment events, but there was no reason to expect any systematic bias in our observations because treatments were randomly distributed. Moreover, the possibility of missed observations declined substantially during the course of the experiment as the number of unmated pairs decreased and fewer arenas were under observation.

Experiment 2: Female Hunger and Female Choice

Experimental trials were carried out over 7 days between 19 and 30 July 1998 and again on 2 days in July 2000 (14 and 18 July). The experiment followed that of a mixed or split-plot design with male phenotype nested within female hunger state. Each female in the fed treatment (*N*=53) and each female in the nonfed treatment (*N*=55) was paired with two males, one large and one small. Mating arenas were observed until termination of copulation or for a maximum of 3 h. Near continuous observation was achieved by having each observer (total of four observers) observe a maximum of three mating arenas per trial. Treatments were evenly distributed among observers and, in some cases, more than one experimental trial was conducted on the same day.

In order to obtain at least one mating for each male phenotype within each female hunger treatment, we adopted a 5-h female starvation period. Previous work and pilot studies indicated that females starved for longer than 6 h expressed extreme reluctance to mate, and those starved for less than 3 h did not vary their mating rate relative to fed females (Jamieson & Scudder 1977; Rowe 1992). All males in the experiment were fed immediately prior to the observation period.

We used a qualitative method for selecting extreme male phenotypes from the tails of the natural size distribution. All males were visually divided into groups of small and large body size. The smallest and largest individuals within these two groups were further sorted in the same manner to yield a total of four size classes. Males in the extreme small and large size classes were individually marked using gold and silver permanent ink markers and used in the experiment. At the end of each trial, we preserved males in 95% ethanol to confirm our qualitative size estimates with quantitative measurements of males. We used digitizing software to record two independent measurements of total body length, from the tip of the head to the end of the last nongenital segment, and calculated mean body size for large and small males.

In experiments conducted in July 1998, we measured male harassment rate and unsuccessful struggle duration for each replicate and calculated the means and standard errors of these variables per male per replicate. We also recorded the phenotype of the first male to copulate, copulation duration and guarding duration. Replicates were observed continuously until the end of copulation or for a maximum of 3 h. The experiments in July 2000 served to increase our sample size of mating pairs and thus, we did not record harassment and unsuccessful struggle data during this experiment.

Analyses

All statistical analyses were performed using SYSTAT 5.1 (Wilkinson 1988). In experiment 1, we conducted two-way analyses of variance (ANOVA) to test for differences in copulation duration and guarding duration among treatments. All variables were transformed using the natural logarithm to minimize heteroscedasticity and meet statistical assumptions (Hartley's test). For experiment 2, we followed a split-plot or mixed experimental design. We considered each treatment pail as a statistical replicate and male body size was a nested factor within female hunger state. Therefore, male harassment, from both large and small males, was treated as a repeated measure for each subject female where the within-subject factor was male body size and the between-subject factor was female hunger state. We conducted repeated measures ANOVAs to test for differences in male harassment rates and unsuccessful struggle duration between female treatments and male phenotype. In both experiments, we tested for dependence of mating rate on experimental factors using log-likelihood ratios and chi-square tests (Zar 1984). Analyses revealed nonsignificant observer and block effects for all experiments and thus, results represent combined data among observers and among trial days.

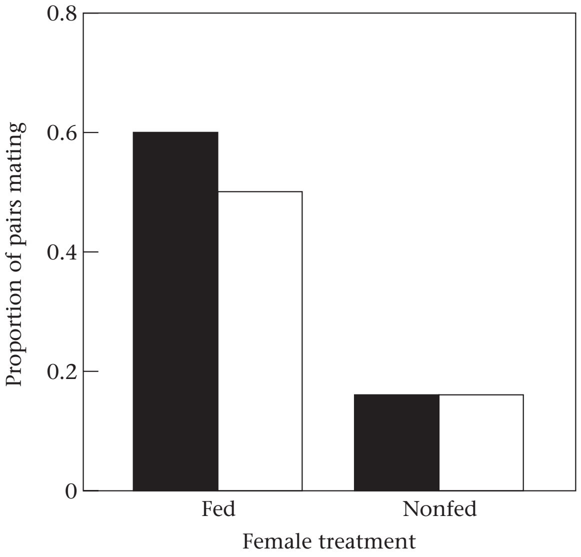

Figure 1. The effect of male and female feeding treatments on the proportion of pairs to mate in experiment 1. ■: Fed males; □: nonfed males.

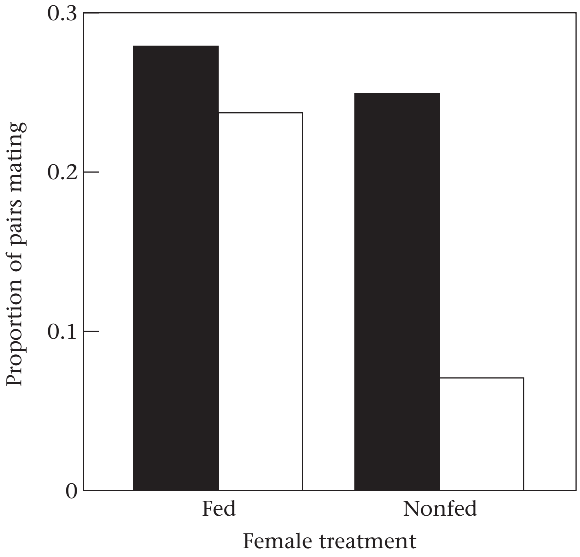

Figure 2. The effect of hunger and male phenotype on the proportion of pairs to mate in experiment 2. ■: Large males; □: small males.

RESULTS

Experiment 1: Hunger in Both Sexes

Hunger affected female, but not male, mating rate. The majority of pairs in the fed female treatments mated during the observation period (Fed$_{♀}$Fed$_{♂}$: 15/25, Fed$_{♀}$Nonfed$_{♂}$: 12/24). In contrast, very few pairs in the nonfed female treatment mated (Nonfed$_{♀}$Fed$_{♂}$: 4/25, Nonfed$_{♀}$Nonfed$_{♂}$: 4/25). The log-likelihood ratio model for mating frequency was significant ($\chi^2_3=17.74$, $P<0.001$) and chi-square tests revealed a significant female treatment effect ($\chi^2_1=10.31$, $P=0.001$) but no significant male effect ($\chi^2_1=0.26$, $P=0.61$) (Fig. 1).

Male harassment rate and copulation duration did not vary with female or male food treatments and there was no significant interaction (Table 1). Guarding duration was not analysed because no pairs guarded in either nonfed female treatment and only three pairs guarded in each of the fed female treatments.

Experiment 2: Hunger in Females and Female Choice

We combined data from the 1998 and 2000 experiments because results did not vary between years. The mean body length of large males was 6.30 ± 0.03 mm ($N=106$) and that for small males was 6.0 ± 0.03 mm ($N=108$). Male body size differed significantly between male phenotypes (Student's t test: one-tailed $t_{212}=8.86$, $P<0.0001$) and represents a change of about 5% in body size. This difference compares with other data for size variation in *G. buenoi* (Rowe & Arnqvist 1996; personal observation).

Hungry females again reduced their mating frequency and small males were at a particular mating disadvantage when females were hungry and reluctant to mate (Fig. 2). The mating frequencies of fed and nonfed females with small and large males (subscripts S and L) were: Fed$_L$=15/53, Fed$_S$=14/53, Nonfed$_L$=13/55, Nonfed$_S$=4/55. The log-likelihood ratio model explained a significant amount of variation in mating frequency ($\chi^2_3=30.79$, $P=0.046$). Large males mated more than small males in the nonfed female treatment ($\chi^2_1=4.76$, $P=0.029$) but there was no difference between large and small male mating frequencies in the fed female treatment ($\chi^2_1=0.03$, $P=0.853$).

Male harassment rate and unsuccessful struggle duration did not vary significantly between female feeding treatments or between male phenotypes within a food

Table 1. Mating behaviour as a function of food treatment

Dependent variable	Fed$_{♀}$ Fed$_{♂}$	Fed$_{♀}$ Nonfed$_{♂}$	Nonfed$_{♀}$ Fed$_{♂}$	Nonfed$_{♀}$ Nonfed$_{♂}$	*df*	*F*	*P*†
Harassment rate (number/h)*	1.83	2.36	1.86	2.06	1,95	0.15	0.70^{a}
SE range	(1.6–2.1)	(2.0–2.8)	(1.6–2.2)	(1.8–2.4)	1,95	1.38	0.24^{b}
N	25	24	25	25	1,95	0.25	0.62^{c}
Copulation duration (min)*	8.20	8.19	8.12	8.50	1,31	0.01	0.92^{a}
SE	(0.78)	(0.87)	(1.5)	(1.5)	1,31	0.02	0.88^{b}
N	15	12	4	4	1,31	0.02	0.87^{c}

*Values are backtransformed means. Test statistics are from ANOVAs.
†Superscript letters 'a', 'b' and 'c' correspond to female, male and interaction effects, respectively.

Table 2. Mating behaviours of large and small males in fed and nonfed female treatments

	Fed♀		Nonfed♀				
Dependent variable	Large	Small	Large	Small	*df*	*F*	*P*†
Harassment rate (number/h)*	3.38	3.28	4.00	3.45	1,62	2.73	0.10^{a}
SE range	(2.9–3.9)	(2.9–3.8)	(3.5–4.6)	(3.0–4.0)	1,62	0.06	0.81^{b}
N	31	31	33	33	1,62	1.92	0.17^{c}
Unsuccessful struggle duration (s)*	10.09	6.06	6.12	5.42	1,40	1.54	0.22^{a}
SE range	(8.5–12.0)	(5.3–7.0)	(4.6–8.1)	(4.3–6.8)	1,40	3.15	0.08^{b}
N	12	17	25	25	1,40	1.86	0.18^{c}
Copulation duration (min)*	5.86	6.06	8.04	9.00	1,28	1.58	0.22^{d}
SE	(4.8–7.2)	(4.9–7.5)	(6.2–10.5)	(6.0–13.4)	1,28	0.07	0.80^{e}
N	12	10	7	3	1,28	0.02	0.89^{f}
Guarding duration (min)*	10.59	12.53	9.65	2.12	1,11	0.96	0.35^{d}
SE range	(4.0–27.8)	(6.7–23.5)	(5.1–25.3)	(0.6–6.9)	1,11	0.50	0.50^{e}
N	3	7	3	2	1,11	0.20	0.66^{f}

*Values are backtransformed means.

†Superscript letters 'a', 'b' and 'c' correspond to female treatment, male phenotype and interaction effects, respectively, for repeated measures ANOVA; superscript letters 'd', 'e' and 'f' correspond to female treatment, male phenotype and interaction effects, respectively, for ANOVA.

treatment (Table 2). Interestingly, however, the increase in mean unsuccessful struggle duration of large males approached significance (ANOVA: $F_{1,40}$=3.15, P=0.08). As in experiment 1, copulation duration did not vary by female hunger and there was no effect of female food treatment on guarding duration (Table 2). Absence of a female hunger effect on these variables could not be explained by small sample sizes in the nonfed treatment because grouping male phenotypes within female treatments did not change the results qualitatively. Mean copulation duration was greater for small than large males, but this difference was not significant (Table 2), and guarding duration did not differ between male sizes.

DISCUSSION

Any condition (ecological, physiological or other) that alters mating rate has the potential to affect mating patterns and ultimately sexual selection (Wiley & Poston 1996). Our results demonstrate that one element of female state (hunger) reduces mating rate, and intensifies sexual selection for male body size. These results are connected by their shared dependence upon female resistance. Hunger affects female resistance, which affects mating rate, and determines the strength of sexual selection on male size. There is no indication that females are less reluctant to mate with large males; instead large males appear better able to overcome female resistance. Our results, thereby, support passive (or indirect), rather than active choice for large male size. Below, we discuss each of these findings in turn.

Mating Rate

Female hunger in *G. buenoi* decreased mating rate dramatically, while male hunger had no effect. These results replicate, to a large degree, earlier experiments conducted on this species in a British Columbia population (Rowe 1992) and the main conclusions of that work are supported here. First, female interests appear to play a major role in determining mating frequency and female state is an important determinant of female interests. Foraging by females conflicts with mating (Rowe 1992, 1994), and therefore, hungry females are expected to be more reluctant to mate. In contrast, we can provide no evidence that male hunger state affects male behaviour. We also found no effect of male or female hunger on copulation and guarding duration, which is in accord with the earlier experiments on this species. Results with *G. buenoi* contrast with an earlier study of a stream dwelling species, *Aquarius remigis*, where female hunger increased female mating rate (Rowe et al. 1996). In *A. remigis*, in contrast to *G. buenoi*, mating may actually increase foraging rates because food is localized and male harassment of single females excludes them from prime foraging sites (for further discussion, see Rowe et al. 1996).

In contrast to earlier work on this species (Rowe 1992), the current experiments provide direct evidence for the hypothesis that changes in mating rate with female hunger result from changes in female resistance. In this species and many other water striders, most mating begins after short struggles, where longer struggles are associated with unsuccessful mating attempts by males (Rowe et al. 1994; Arnqvist 1997). Increased mating frequency of satiated females may result either from females employing fewer long struggles, or from males investing more effort in overcoming these struggles. Males may invest more in satiated females because these females have distended abdomens, which is also an indicator of high fecundity (personal observation; see also Bonduriansky & Brooks 1998). However, if increased mating frequency of satiated females resulted from increased male effort, we would expect that struggle durations would increase in female satiated treatments. We found no such effect. Mean unsuccessful struggle duration (and male harassment rate) was unaffected by female hunger (Tables 1, 2). These results are in accord with earlier studies (Arnqvist 1992; Rowe 1992; Lauer

1996; Weigensberg & Fairbairn 1994), suggesting that females increase mating frequency by increasing the employment of very short or no struggles.

Female Hunger and Sexual Selection on Male Body Size

Sexual selection for large male size is common in water striders, yet the strength of selection is highly variable between species and between populations within species (reviewed in Arnqvist 1997). Both the cause and variability in selection for size requires explanation. Our results address both of these issues.

There are two alternative hypotheses for selection for large size. First, females may reduce struggle duration when a mating attempt is made by a large male, perhaps because large size indicates good genes in males. This may be referred to as active choice (Parker 1983). Alternatively, female resistance may be independent of male phenotype, but large males may be better able to overcome resistance (passive choice). Our results support the passive choice hypothesis for two reasons. First, when reluctance of females was low (satiated females), there was no significant advantage for large males, but when reluctance was high (hungry females), large males were preferred (Fig. 2). These results are expected under passive choice because large size advantage in overcoming resistance should be an increasing function of the degree of resistance. Such a pattern is not expected under active choice, because there is no a priori reason to expect that female preference would be a function of the overall level of female resistance. Second, under passive choice we would expect large males to withstand struggles for longer periods than small males. Our data tend to support this view. Mean struggle duration, in struggles that did not lead to mating, was greater in large than small males, although the effect was not significant at the $P<0.05$ level (Table 2, $P=0.08$). It seems, at least in this species, that increasing energetic costs of struggles as a function of increasing male size does not explain large-male mating advantage. Taking into consideration other studies of choice for various grasping traits in male water striders (Arnqvist 1989; Weigensberg & Fairbairn 1996; Westlake et al. 2000) and findings in other groups (Diptera: Crean & Gilburn 1998), we propose the passive choice model as a viable explanation for large-male advantage in this system. Furthermore, passive female choice is more likely to operate in systems where females change their level of resistance based on convenience.

The high interpopulation variability observed in large-male mating advantage of water striders has been attributed to variation in local environmental conditions (e.g. density, operational sex ratio, predation; Arnqvist et al. 1996; Rowe & Arnqvist 1996). Our results, demonstrating a significant effect of female hunger on preference for large male size, offer strong support for this view. Any local environmental conditions that affect female hunger levels are expected to affect the intensity of large-male mating advantage. There is also high intrapopulation variation in copulation and guarding duration. Previous work suggests that some of this variability can be explained by environmental conditions and male body size. For example, when the operational sex ratio is male biased, copulation duration typically increases (Rowe 1992). Also, small males copulate longer than large males, but large males guard for longer (Rowe & Arnqvist 1996; Arnqvist & Danielsson 1999). This variation may contribute to interpopulation variation in observed large-male mating advantage. Although small males in the current experiments tended to copulate for longer than large males, the difference between these durations was small and statistically nonsignificant. Guarding was infrequent, highly variable in duration, and no male size effects were detected.

In conclusion, we have demonstrated that local ecological conditions, through their effect on female hunger, can have strong effects on mating rates and sexual selection for large male size. These effects both result from an effect of hunger on female reluctance to mate. The level of female hunger is expected to depend upon all those environmental conditions known to affect per capita food supply (e.g. density). Therefore, we should expect high interpopulation variation in mating frequencies and in the strength of sexual selection. This view is not limited to water striders (e.g. Crean & Gilburn 1998; Dunn et al. 1999). Persistent harassment by males and resistance by females is a common feature in mating systems (Clutton-Brock & Parker 1995). Where the payoff of resistance to females depends upon local conditions, similar interpopulation variation in sexual selection is possible.

Acknowledgments

Our thanks to G. Arnqvist, R. Bonduriansky and D. Jackson for advice and comments on the manuscript. Experiments were performed with the help of Y. Cheng, M. Tseng and K. Westlake. This reserach was supported by an NSERC grant to L.R. and University of Toronto Fellowships to A.O.

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