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Analysis of the causal components of assortative mating in water striders

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Abstract Field studies demonstrate that natural populations of a group of water striders (Heteroptera: Gerridae) that share a common mating system are characterized by weak assortative mating by size and by large sizes of mating males and females relative to single individuals. This study presents an experimental assessment of the components of mating that may contribute to these mating patterns. The effects of male and female body size on each of three components of mating were studied in three water strider species in the laboratory. Large females of all three species mated more frequently, copulated for longer and were guarded longer than small females. Large males mated more frequently than small males in all three species, and also guarded females for longer in the two species where the average of mate guarding was long. However, we found an antagonistic effect of male size on copulation duration: small males copulated for longer than large males in all three species. We show that the combined effects of these size biases mimic the mating patterns found in the wild, e.g. weak and variable assortative mating, and stronger and less variable size ratios of mating versus non-mating females relative to males. We suggest that the antagonistic effects of male size on copulation and guarding duration may be a key source of interpopulational variation in assortative mating and sexual selection on male size. Further, neither spatial or temporal covariation in size, nor mechanical constraints, caused the assortative mating observed here in this group of water striders. Some combination of male and female choice (either active or passive forms) of large mates and male-male exploitation competition for mates play potentially important roles in producing population level assortative mating in water striders.

Key words Assortative mating · Body size · Mating behaviour · Gerridae · Sexual selection

Introduction

Assortative mating by size, or homogamy, is one of the commonest mating patterns in natural populations and has significant evolutionary implications (Ridley 1983; Crespi 1989). It is defined, simply, as a positive correlation between the body sizes of mating males and females. Despite its prevalence, the causes of assortative mating are unresolved in all but a few cases. Many mechanisms may lead to this pattern, so inferences of process from pattern are typically weak. For example, assortative mating may result solely from spatial or temporal covariances with body size in the wild. This mechanism can not be ruled out with only data collected on the sizes of mating pairs in the wild, and these are the sorts of data that are typically collected in field studies. A laboratory study, however, can potentially rule out such covariances.

We suggest that processes that lead to the pattern of assortative mating should be studied at two levels. First, size biases in the components of mating that lead to the pattern should be identified. Second, processes (e.g., mate choice) that lead to size biases in each contributing component of mating should be identified. For example, analysis of assortative mating and the size of mating and non-mating individuals may lead one to conclude that matings are biased towards large males and females. However, the association of large males

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with large females may result from size biases in the frequency of contact between these types, their mating frequency, or their mating duration. Identification of these biases identifies which component or components of mating behavior operate to generate assortative mating. Similarly, the demonstration of female choice for large male size in mating frequency may actually contribute little to assortative mating if size bias in guarding duration is the main contributor to the overall frequency of occurrence of pairs. Interpretation may be further complicated if the relative contribution of mating frequency and guarding duration to frequency of occurrence of pairs varies with ecological conditions. This is not a minor problem, because such variation is quite common. Guarding duration is known to depend on the local operational sex ratio in a variety of species for a variety of reasons (Sillen-Tullberg 1981; Clark 1988; McLain 1989; Moore 1989; Telford and Dangerfield 1990; Arnqvist 1992a; Rowe 1992). A laboratory study can potentially identify size biases associated with each component of mating and therefore elucidate how they may interact to produce varying degrees of assortative mating. Therefore, three sorts of studies (field collections, component identification and mechanistic) are often required to yield a complete understanding of assortative mating. The current study centres on the identification of the components of mating that contribute to assortative mating.

Previously, we have analyzed the pattern of assortative mating in 45 natural populations of seven water strider species (Hemiptera: Gerridae) that share a common mating system (Arnqvist et al. 1995). This study revealed weak positive assortative mating and a larger size of mating compared to non-mating individuals in both sexes. Water striders mate multiply and mating includes a copulation and guarding phase (reviews in Rowe et al. 1994; Spence and Andersen 1994; Arnqvist 1995). Therefore, the observed pattern of assortative mating in water striders may potentially result from either one or a combination of size biases in mating frequency, copulation duration or guarding duration. Moreover, the contribution each of these components to the mating activity of water striders is sensitive to a variety of environmental conditions (Rowe et al. 1994).

Here we report a laboratory study of assortative mating in three of these water strider species. The purpose of the study is fourfold. First, we use a laboratory setting to determine if assortative mating occurs in the absence of any temporal or spatial covariances in body size that may occur in natural populations. Second, we identify the size biases associated with each of the three components of mating (mating frequency, copulation duration and guarding duration) and assess their contribution to size assortative mating. Third, we determine if the three focal species share qualitatively similar size biases as predicted from their shared mating system. Fourth, we use these data to explore sources for the strength and variability of mating patterns found in the wild.

Methods

The experiment described here was replicated for each of three species (*Gerris lateralis*, *G. buenoi*, and *G. lacustris*). The mating behavior of these species is described in detail in Arnqvist (1988). Rowe (1992), and Vepsäläinen and Savolainen (in press) respectively, and all three species share a common mating system (type I *sensu* Arnqvist 1995; see also Andersen 1994). Sexual harassment of females by males is frequent. Males attempt to initiate matings by grasping females. If a grasp is achieved, then pairs engage in a pre-mating struggle during which the male attempts to achieve intromission. Copulation occurs only if the male endures or overcomes female resistance. Copulation lasts about 5–20 min and is followed by a guarding phase of greatly varying duration (< 1 min to several hours). During the guarding phase, the male rides on top of the female without genital contact. Mating is typically terminated with a post-mating struggle initiated by the female.

The basic experimental design involved three components: (1) selecting the largest and smallest males and females from a sample, (2) placing these individuals in laboratory enclosures for a set period of time, and (3) determining size biases in the frequency of mating, copulation duration, guarding duration, and total duration of mating. Water striders were collected with hand nets in early June 1993 in the University of British Columbia Botanical Gardens, Canada (*G. buenoi*) and in the River Tväran, Västerbotten, Sweden (*G. lacustris* and *G. lateralis*). Twice the number of individuals required for the experiment for each species were collected. For each species and sex, individuals from the tails of the size distribution were selected for use in the experiments by the following procedure. We first subjectively divided each sample into two groups representing small and large individuals. For each of these two groups, we repeated this division. By this subjective procedure, four groups (small, large; male, female) of each species were selected that were meant to represent the approximate 25% tails of the natural size distribution of each sex. We chose this method to increase the detectability of any size biases, and to simplify subsequent statistical analyses. Following the experiment, ten randomly chosen individuals of each species, sex and size category were preserved in 70% alcohol. These individuals were subsequently measured with an ocular micrometer to provide an objective estimate of size differences between our small and large categories.

All water striders were individually marked with paint and introduced into rectangular (surface area = 0.5 m^2; *G. buenoi*) or circular pools (surface area = 0.79 m^2; *G. lacustris*; *G. lateralis*). For *G. buenoi*, eight males (four small, four large) and four females (two small, two large) were added to each pool. For *G. lacustris* and *G. lateralis*, four males (two small, two large) and four females (two small, two large) were added to each pool. Twenty replicate pools were set up for each species. Each individual was used only once. Ambient temperature was 21 ± 2°C. Each pool was aerated, contained floating styrofoam for oviposition and resting sites, and was regularly replenished with frozen fruitflies for food.

Mating status (single, copulating or guarding) of each individual in each replicate was recorded in a series of spot checks, conducted over two observation periods of 4 h for each replicate. Spot checks occurred at 10-min intervals for *G. buenoi* and 15-min intervals for *G. lacustris* and *G. lateralis*. At the beginning of each observation period, any individuals that were mating were separated, so that each observation period began with only single individuals. The temporal spacing of spot checks may have resulted in some very short matings being missed. However, continuous observation of pools suggests that although such short matings occur, they are very rare under these experimental conditions.

For each of the four possible size combinations of mates in each replicate pool, the mean values of mating frequency, copulation duration, guarding duration, and total mating duration (copulation + guarding duration), were calculated and used as dependent variables in subsequent analyses. For each of the three species, there were 20 replicate pools. We included a measure of total mating duration because it has utility for comparison with other water strider species; in at least one commonly studied species (*Aquarius remigis*) copulation and guarding phases are indistinguishable (Clark 1988; Rubenstein 1989). We also calculated the proportion of the total mating observations in each pool (total mating activity) that each of the four possible male/female size combinations accounted for. This statistic incorporates both the size biases in mating frequency and in mating duration. It is analogous to taking an average cross-sectional sample of mating pairs in pools, as one would in a field survey of non-random mating, and is therefore a directly comparable statistic to those acquired in typical field studies of assortative mating.

Our experimental design treats each pool ($n = 60$), rather than each individual ($n = 400$) or mating event (several hundred), as the replicate. The design thus avoids the pseudoreplication that would result from multiple observations on individuals or on pools. For example, if we see a total of 20 matings in a pool containing five individuals of each size and each sex, then the overall mean individual mating frequency is 2 for each sex. If 14 of these matings involved large males and females, and 2 for each of the remaining three size combinations, then the average mating frequency for the four size combinations is 2.8, 0.4, 0.4, 0.4, respectively. Moreover, our statistical analysis would indicate significant positive effect of male and female size on mating frequency. Statistical analyses were performed with a nested repeated measures analysis of variance (i.e. a nested within subjects design; Kirby 1993). In this design, the experimental pools are considered subjects. The between subjects factor (nested) is species and the within subjects factors are male and female body size. Prior to analysis, proportions were arcsine transformed. The remaining variables were transformed following the method of Berry (1987). Data for each variable were transformed using $X' = \log(X + c)$, where X is the original value of the datum and c is a constant chosen to minimize the sum of the absolute values of skewness and kurtosis of the residuals from each model.

Determination of quantitative species effects on the magnitude of mating components was not a primary goal of our experiment. Given that the experimental conditions varied (sex ratio and density) between *G. buenoi* on one hand and *G. lacustris* and *G. lateralis* on the other, true species effects can only be reliably interpreted from differences between *G. lacustris* and *G. lateralis*. Therefore, species comparisons with post-hoc contrasts were restricted to the latter pair. Our statistical analysis controls for quantitative differences between species in the overall magnitudes of each variable. This allows us to focus on our primary goals of detecting size biases in each component and species effects on these biases. A significant species by size (either male or female) interaction term in our analysis indicates that the size biases differ among species. In these cases we show figures for each species. Likewise, if these interaction terms are not significant, we show the combined species mean in figures since size biases do not differ among species.

Results

Size categories

Post hoc measurement of the sub-set of experimental individuals revealed that our subjective method of creating two groups of each sex that differed significantly in size was successful for each species (Table 1).

Mating frequency

Large individuals of both sexes mated more frequently than small individuals, and this effect was consistent across all three species (Fig. 1, Table 2). Averaged across all species, large males mated 15% more frequently than small males and large females mated 17% more frequently than small females. The mean number of matings per pool was 15.7 (SE = 1.00) for *G. lacustris* and 14.6 (SE = 0.81) for *G. lateralis*, and these values did not differ significantly ($t = 0.851$, $df = 38$, $P = 0.400$). The mean number of matings per pool for *G. buenoi* was 22.6 (SE = 2.35). Note that this summary number includes all size classes of pairs. Mating frequencies shown in Fig. 1 are means for each of the four possible size combinations of pairs.

Copulation duration

Large females copulated for significantly longer than small females, but small males copulated for significantly longer than large males (Fig. 1, Table 2). These effects were consistent across species. Averaged across species, large females copulated for 17% longer than small females, and large males copulated for a 16% shorter period than small males. The mean copulation duration was 23.9 min (SE = 0.94) for *G. lacustris* and 19.5 min (SE = 1.47) for *G. lateralis*, and these values differed significantly ($t = 2.558$, $df = 38$, $P = 0.015$). The mean copulation duration of *G. buenoi* was 10.3 min (SE = 0.32).

Mate guarding duration

There were significant positive effects of size for both sexes on guarding duration, however, there were also

Table 1 Mean body size of males and females in the large and small size categories used in the experiments ($n = 10$ in all cases), and two-tailed probabilities of differences between size categories (*t*- tests)

Species	Sex	Mean body size (mm) ± SE Large ind.	 Small ind.	*P*	Size ratio (large/small)
Gerris buenoi	Male	7.02 ± 0.06	6.77 ± 0.03	< 0.005	1.04
	Female	7.79 ± 0.06	7.26 ± 0.07	< 0.001	1.07
G. lacustris	Male	8.25 ± 0.06	7.77 ± 0.12	< 0.005	1.06
	Female	9.32 ± 0.15	8.49 ± 0.11	< 0.001	1.10
G. lateralis	Male	8.79 ± 0.10	8.14 ± 0.10	< 0.001	1.08
	Female	9.86 ± 0.10	8.99 ± 0.09	< 0.001	1.10

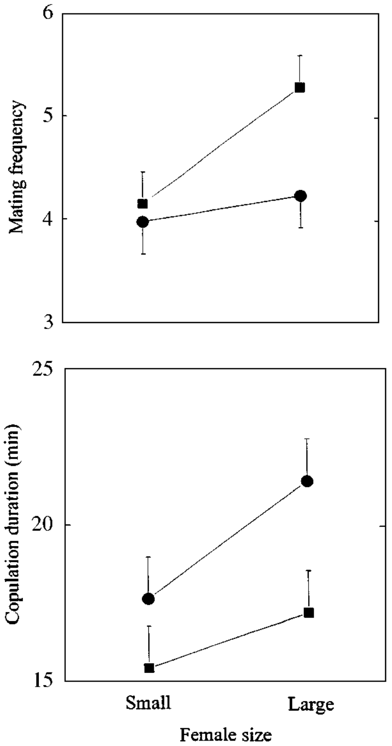

Fig. 1 The effects of male and female body size on mating frequency (*upper panel*) and copulation duration (*lower panel*) for all three species of water striders. *Circles* represent small males and *squares* represent large males. *Error bars* represent 1 SEM

significant interaction terms that reflected differences among the species and in the strength of the female size effect (Fig. 2, Table 2). These interaction terms resulted from extremely short and size-independent guarding durations in *G. lacustris*, and a stronger large female bias when paired with large rather than small males, in the remaining two species (Fig. 2). Averaged across species, large females were guarded for 42% longer than small females and large males guarded for 93% longer than small males. The mean duration of mate guarding was 0.5 min (SE = 0.21) for *G. lacustris* and 40.4 min (SE = 4.38) for *G. lateralis*, and these values differed significantly ($t = 9.118$, $df = 38$, $P < 0.001$). The mean mate guarding duration of *G. buenoi* was 20.7 min (SE = 1.95).

Total mating duration

These results reflect the combined effect of copulation and guarding durations. There were significant positive effects of female and male size on total mating duration, as well as significant interactions between female and male size, and these factors and species (Fig. 2, Table 2). These interactions resulted from the combination of extremely short guarding durations in *G. lacustris* and the relatively long durations of small males observed in copulation duration (Fig. 2). In *G. buenoi* and *G. lateralis* the male size effects in copulation and guarding duration oppose one another (Figs. 1 and 2). However, because guarding durations in these species are long relative to copulation duration, the total duration of mating is greater in large males than small males (Fig. 2). In contrast, guarding durations in *G. lacustris* were short, and therefore copulation duration dominates the analysis of total mating duration in this species. Averaged across species, total mating duration of large females was 29% longer than that of small females, and total mating duration of large males was 30% longer than that of small males. The mean total duration of mating was 24.5 min (SE = 0.96) for *G. lacustris* and 59.9 min (SE = 4.37) for *G. lateralis*, and these values differed significantly ($t = 7.905$, $df = 38$, $P < 0.001$). The mean total mating duration of *G. buenoi* was 30.9 min (SE = 1.95).

Table 2 Analysis of variance results for the effects of species, male size and female size on mating frequency, copulation duration, guarding duration, total mating duration and the proportional representation in the total mating activity. These values represent the results of five independent ANOVAs. Each variable is defined in the text

Source	*df*	Mating frequency		Copulation duration		Guarding duration		Total Mating duration		Prop. rep. in total mating activity	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Between subjects											
Species	2	8.43	0.001	8.43	<0.001	109.01	<0.001	46.87	<0.001	0.38	0.682
Error	57										
Within subjects											
Male size	1	5.16	0.027	7.58	0.008	4.58	0.04	12.75	0.001	17.86	<0.001
Male size species	2	0.27	0.764	0.10	0.903	2.21	0.12	1.00	0.374	0.66	0.374
Error	57										
Female size	1	4.53	0.038	4.72	0.034	27.10	<0.001	13.26	0.001	19.25	<0.001
Female size species	2	0.70	0.502	0.84	0.438	11.27	<0.001	6.17	0.004	1.86	0.165
Error	57										
Male size female size	1	2.14	0.148	0.21	0.646	4.73	0.034	0.94	0.337	3.08	0.085
Male size female size species	2	0.32	0.729	2.03	0.141	3.54	0.036	3.72	0.030	2.13	0.128
Error	57										

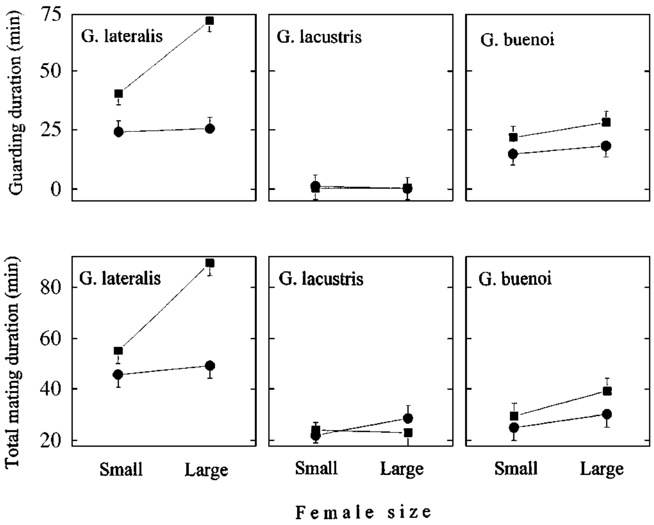

Fig. 2 The effects of male and female body size on mate guarding duration (*upper panel*) and total mating duration (*lower panel*) for each of the three species. *Circles* represent small males and *squares* represent large males. *Error bars* represent 1 SEM

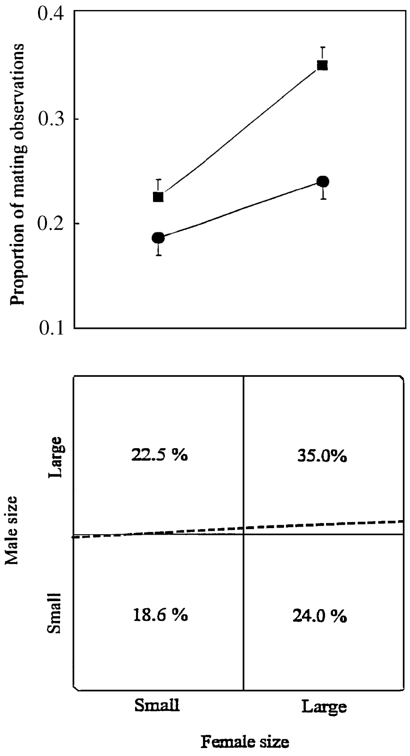

Fig. 3 *Upper panel* shows the effects of male and female body size on the proportion of mating observations (see text for definition) for all three species. *Circles* represent small males and *squares* represent large males. *Error bars* represent 1 SEM. *Lower panel* shows the average frequency of mating observations from each replicate for each of the four possible size combinations of mates. *Dashed line* represents regression line drawn by setting body sizes of males and females as 1 = small, and 2 = large. The statistics correspond to those in Table 2 where both male and female size effects are significant and positive. This line equals the average relationship between the sizes of the sexes that would be obtained from cross-sectional samples of assortative mating in our experimental pools

Proportional representation of mating activity

Large individuals of both sexes were represented in a significantly greater proportion of the total mating observations than were small individuals, and this effect was consistent across all three species (Fig. 3, Table 2). We show the average frequency of mating observations from each replicate for each of the four possible size combinations of mates in Fig. 3 (lower panel). This pattern leads to weak assortative mating, as indicated by the regression drawn from these data. Alternatively, under strong assortative mating, we would expect mating activity to be concentrated in both the upper right and lower left quadrants of Fig. 3 (lower panel). Averaged across all species, large females were represented 44% more frequently in the total mating activity of pools than small females. The corresponding difference for large males is 35%.

Discussion

We have shown that size biases, of varying direction, occur in each component of water strider mating in a laboratory setting. Here we focus on two themes. First, we show how the identification of these size biases in the components of mating contributes to an understanding of patterns of assortative mating in the wild. Second, we use these data to point to the behavioural interactions that must be studied to understand the mechanisms (e.g. mate choice) that lead to observed patterns of assortative mating by water striders in the wild.

The form of assortative mating

Results from this experiment demonstrate that assortative mating in these species arises from the large size of both males and females that are mating relative to those that are single (Fig. 3, Table 2). We have previously distinguished two forms of assortative mating (Arnqvist et al. 1995). The first, “true” assortment, is characterized by a symmetrical distribution of observations around the linear regression describing the effect of female size on male size in mating pairs. The second, “apparent” assortment, is recognized by either increasing or decreasing variance in male size with increasing female size. The evolutionary consequences of apparent assortment differ from those of true assortment (Crow and Felsenstein 1968; Partridge 1983; Arnqvist et al. 1995). Our data allow us to reject apparent assortment as the form of assortative mating in these water striders. We found positive effects of male and female size on mating activity, and no interaction between these effects (Fig. 3, Table 2). These effects are predicted from true, but not from apparent, assortment. Field data similarly support true assortment in this group of insects (Arnqvist et al. 1995).

Size biases and the causal components of mating

Our study demonstrates size biases in both sexes, for all components of mating. Previous studies of water striders have often shown that mating females were larger than single females in field samples (Fairbairn 1988; Arnqvist et al. 1995), and large females mate more frequently under experimental conditions (Krupa and Sih 1993; Batorczak et al. 1994). Similarly, previous studies have often shown positive, but more variable and weaker, effects of male size on mating success (Fairbairn 1988; Sih and Krupa 1992; Krupa and Sih 1993; Arnqvist et al. 1995; Fairbairn and Preziosi 1994). We found positive size effects for females in all three components of mating (mating frequency, copulation duration and guarding duration) that were consistent among all three species. Although the overall effect of male size was positive, the effects were relatively weak and antagonistic among the components of mating. Large males mated more frequently than small males in all three species, and large males guarded longer in the two species in which significant guarding occurred. In contrast, in all three species, small males copulated longer than large males.

The opposing effects of male size on copulation duration versus. mating frequency and guarding duration may offer explanations for both the relatively weak and variable effect of male size on mating success and for the generally weak and variable degree of assortative mating that is characteristic of water striders (Arnqvist et al. 1995). In short, the bias toward large males in the mating sample will depend upon the average ratio of copulation to guarding duration of matings within a population. Smaller ratios predict a stronger bias, because the relative strength of small-male bias in copulation duration will diminish as the ratio declines. Absolute values of all three components of mating are highly dependent upon a variety of local environmental conditions in water striders (reviewed in Rowe et al. 1994). For example, local sex ratio has strong effects on each component of mating (Clark 1988; Arnqvist 1992a; Rowe 1992; Sih and Krupa 1992; Vepsäläinen and Savolainen in press; Weigensberg and Fairbairn 1994) and the ratio of copulation to guarding duration has been shown to depend upon local sex ratio in *G. buenoi* and *G. lacustris* (Rowe 1992; Vepsäläinen and Savolainen in press). Large-male mating advantage in water striders also varies with local environmental conditions (Sih and Krupa 1992; Krupa and Sih 1993). There is good reason to believe that this ratio will be sensitive to many other local environmental conditions. Similar interactions between the environment and mating components may contribute to the variation in assortative mating seen in other taxa.

The relatively long copulation durations of small males are intriguing. The cause is almost certainly the result of a male decision, rather than female choice (it is difficult to imagine why females would allow small males to copulate longer, but allow large males to guard for longer). It may be that, small males require more time to transfer their sperm or to displace the sperm of others as has been predicted and demonstrated by Parker and Simmons (1994) for dungflies. Similarly search times may be greater for small males, and this too leads to longer optimal copulation durations (Parker and Simmons 1994). Our data support this idea because small males have reduced mating frequency, as would be the case if search times were relatively high. On the other hand, it may also represent a conditional strategy to increase total mating duration. Since mating is typically terminated by the female during the guarding phase (Rowe et al. 1994; Arnqvist 1995), small males may extend the copulation phase to delay the time at which they are susceptible to being dislodged. In either case, small males have more to gain from extending the copulation phase than large males.

Fairbairn (1990) suggested that sexual selection for large male size was confined to the larger, less dimorphic water strider species. Data presented here and in Arnqvist et al. (1995) demonstrate that this is not the case. Two of the species included in the current study, and four of the seven species in the accompanying field study, are members of the sub-genus *Gerris*, which is characterized by relatively small body size and relatively strong sexual size dimorphism. We have shown that these species are also characterized by large-male mating advantage.

Causes of assortative mating

Crespi (1989) has classified the potential causes of true assortative mating into a suite of distinct mechanisms; mechanical constraints, spatio-temporal covariation, mate availability and mate choice combined with intrasexual competition for mates.

Mechanical constraints, and spatio-temporal covariation of size classes

Mechanical constraints have been observed or suggested as the cause of assortative mating in several taxa (e.g. Christy 1983; Brown 1993; Reid et al. 1994). Pairings in water striders typically begin and end with a struggle (Rowe et al. 1994; Arnqvist 1995) and mismatched males may be unable to endure such struggles (Jormalainen et al. 1994). Thus, mechanical constraints may contribute to assortative mating in both mating frequency and duration. However, such a mechanism predicts no difference in the size of mating and single individuals at the population level, and is therefore inconsistent with the observed large relative size of mating individuals in both sexes here and in the wild (Arnqvist et al. 1995). Moreover, assortative mating appeared to result primarily from a preponderance of mating activity by large-large (male-female) pairs, rather than from the lack of representation of mismatched pairs, as would be predicted by the mechanical constraints hypothesis (Fig. 3). Under the latter scenario, we would also expect strong interaction effects between male and female size rather than strong main effects of both male and female sizes in our analysis of the effect of size on proportional representation in the overall mating activity of each pool. Instead, we found strong main effects of male and female size and no significant interaction between them (Fig. 3, Table 2). Our experimental design is particularly powerful for detecting such interactions. We used the tails of the size distribution in each sex, thus potential size mismatches in pairing are acute. Therefore, we conclude that any mechanical constraints in pairing are insignificant contributors to the assortative mating observed here.

Assortative mating may result from spatial or temporal covariation in the size classes of males and females (Crespi 1989). However, segregation of adult water striders by size alone cannot explain either large male or female mating bias, which are the primary contibutors to the assortative observed here. We can thus reject this hypothesis for the same reasons that we rejected mechanical constraints (see above). To simultaneously affect large size advantage, it is required that large individuals are segregated into times or spaces in which mating (both frequency and duration) is more likely to occur. We know of no evidence in support of such segregation by size in the wild. Rubenstein (1984) suggested that large individuals of *A. remigis* may concentrate in center zones of streams. Further, these zones may be characterized by high mating activity, resulting from high harassment of females by males (Wilcox 1984; Rowe et al., in press). However, Krupa and Sih (1993) actually found negative size segregation in this species: pools contained mismatched combinations of male and female size classes. Most importantly, however, the scale of our laboratory experiments excludes any such spatial or temporal segregation by size. Therefore, we conclude that spatial or temporal covariation by size is playing no significant role in assortative mating observed in the laboratory.

Mate availability, intrasexual competition and mate choice

The remaining possible causes of assortative mating include mate availability, male-male competition and choice of large mates. A combination of large male advantage in intrasexual competition, and male choice of large females has previously been invoked as the cause of assortative mating in water striders (Fairbairn 1988, following Ridley 1983). However, direct evidence of either process is lacking. There is evidence of female choice for some male traits in water striders (e.g. Arnqvist 1989, 1992b; Rowe 1994). Our data do not apply directly to any of these processes. We suggest that further study should focus on size biases in pre- and postmating struggles and in the transition from copulation to guarding. It is these interactions that determine both the frequency and duration of mating in these species (Rowe et al. 1994; Arnqvist 1995).

Conclusions

In the wild, three patterns of non-random mating by size characterized water striders sharing the type I mating system (Arnqvist et al. 1995). First, size assortative mating was variable and weak, but was overall statistically significant. Second, mating individuals of both sexes were significantly larger than non-mating individuals. Third, the relatively large size of both large male and large female contributed to size assortative mating. In the current study, we found that all three of these patterns occurred in all three species in the controlled environment of the laboratory. In contrast to field studies, we were able to isolate size biases for each sex in each of the three components of mating. Consequently, this study makes four main contributions. First, the concurrence of laboratory and field observations suggests a generality to the causes of assortative mating in this group of insects. Second, this concurrence allows us to eliminate several potential processes that may contribute to assortative mating in the wild. We were able to eliminate mechanical constraints and spatial or temporal covariation as causes of assortative mating in the laboratory. The data are compatible with the combined effects of mate choice, mate availability and intrasexual exploitation competition. Third, variation in the contribution of each component of mating to these patterns, combined with known environmental effects on the expression of each component, lead to new insights into the sources of variation in mating patterns observed in the wild. Finally, we suggest that future studies should focus on transitions to and from copulation and guarding as a means of assessing the contribution of mate choice to assortative mating and its potential adaptive significance.

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