

SEXUALLY ANTAGONISTIC COEVOLUTION IN A MATING SYSTEM: COMBINING EXPERIMENTAL AND COMPARATIVE APPROACHES TO ADDRESS EVOLUTIONARY PROCESSES

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Abstract.—We combined experimental and comparative techniques to study the evolution of mating behaviors within a clade of 15 water striders (*Gerris* spp.). Superfluous multiple mating is costly to females in this group, and consequently there is overt conflict between the sexes over mating. Two alternative hypotheses that could generate interspecific variation in mating behaviors are tested: interspecific variation in optimal female mating rate versus sexually antagonistic coevolution of persistence and resistance traits. These potentially coevolving traits include male grasping and female antigrasping structures that further the interests of one sex over the other during premating struggles. Both processes are known to play a role in observed behavioral variation within species. We used two large sets of experiments to quantify behavioral differences among species, as well as their response to an environmentally (sex-ratio) induced change in optimal female mating rate. Our analysis revealed a large degree of continuous interspecific variation in all 20 quantified behavioral variables. Nevertheless, species shared the same set of behaviors, and each responded in a qualitatively similar fashion to sex-ratio alterations. A remarkably large proportion (> 50%) of all interspecific variation in the magnitude of behaviors, including their response to sex ratio, could be captured by a single multivariate axis. These data suggest tight coevolution of behaviors within a shared mating system. The pattern of correlated evolution was best accounted for by antagonistic coevolution in the relative abilities of each sex to control the outcome of premating struggles. In species where males have a relative advantage, mating activity is high, and the opposite is found in species where females have gained a relative advantage. Our analyses also suggested that evolution has been unconstrained by history, with no consistent evolutionary tendency toward or away from male or female relative advantage.

Key words.—Arms races, Gerridae, macroevolution, mating systems, sexual conflict, sexual selection.

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Research on sexual selection and mating systems is increasingly focused on sexual conflict and the resulting potential for antagonistic coevolution between the sexes. A diverse array of male and female traits (morphological, behavioral, and physiological) that further the interests of one sex over the other have the potential to coevolve antagonistically. These include subtle signal-reception systems involving ejaculate components of males and receptors in females (e.g., Chapman et al. 1995; Wolfner 1997; Clark et al. 1999; Andrés and Arnqvist 2001), coercive behaviors (reviewed in Clutton-Brock and Parker 1995), and overt grasping and antigrasping structures of males and females (e.g., Arnqvist 1989a; Thornhill and Sauer 1991; Arnqvist and Rowe 1995; Sakaluk et al. 1995). Sexual conflict is now viewed as having the potential to be a preeminent force driving the evolution of mating rate and those traits affecting this rate (Parker 1979; Gowaty 1996; Holland and Rice 1998; Partridge and Hurst 1998; Arnqvist and Nilsson 2000). Despite its potential importance, we have little direct evidence that such conflict has played a significant role in the evolutionary dynamics of mating systems or even mating rates.

Empirical studies have largely followed three main approaches. Economic studies have documented the divergent interests of the two sexes within mating interactions (e.g., Rowe et al. 1994; Chapman et al. 1995; Choe and Crespi 1997; Clutton-Brock and Langley 1997; Civetta and Clark 2000). Functional studies have documented the function of a variety of traits that appear to have evolved in response to

sexual conflict over mating and/or male harassment of females (Arnqvist 1989a; Arnqvist and Rowe 1995; Sakaluk et al. 1995; Crean and Gilburn 1998). Finally, studies of experimental evolution have documented the possibility and short-term course of sexually antagonistic coevolution of mating interactions (Rice 1996, 1998; Holland and Rice 1999). In combination, these studies confirm that the interests of the sexes in mating interactions diverge, both sexes have evolved traits to further their own interests in mating, and evolution of these traits can be rapid. However, they do not speak to the question of how important sexual conflict is in the diversification of mating systems in the wild.

Understanding the diversification of mating systems requires quantitative studies of multiple related species in light of a phylogenetic hypothesis (Felsenstein 1985; Brooks and McLennan 1991; Harvey and Pagel 1991). Thus far, macroevolutionary studies of sexual conflict have focused on morphological traits involved in reproduction, rather than the mating system itself (e.g., Pitnick et al. 1999; Presgraves et al. 1999; Westlake et al. 2000; Arnqvist and Rowe 2002a). The lack of such studies may result, in part, from inherent difficulties in conducting comparative studies of potentially plastic suites of behaviors. Although difficult, such behavioral studies are not impossible, as evidenced by analogous studies of signal-receiver behaviors in mating systems (e.g., Basolo 1990, 1996; Ryan 1990, 1998; McLennan 1996, 2000; Uy and Borgia 2000).

The primary aim of this paper is to assess the importance

of sexual conflict in the evolution of mating interactions in the water strider genus *Gerris* (Insecta: Heteroptera). More traditional views of mating systems focus on variance in the external ecological setting as the force driving evolutionary change (Emlen and Oring 1977; Vehrencamp and Bradbury 1984; Davies 1991; Arnold and Duvall 1994; Rowe et al. 1994). However, antagonistic coevolution of persistence and resistance traits may lead to the rapid evolution of mating behaviors, even in the absence of any change in the ecological setting (Parker 1979, 1983a; Hammerstein and Parker 1987; Holland and Rice 1998; Parker and Partridge 1998; Rice 1998; Gavrillets 2000; Gavrillets et al. 2001). These two views of the evolution of mating systems make contrasting predictions for the evolutionary covariance between mating behaviors in *Gerris* spp.

There is overt conflict over mating rate in many water striders and female mating frequencies can be dramatically greater than necessary for fertilization of eggs (reviews in Rowe et al. 1994; Arnqvist 1997). Males frequently harass single females by chasing, lunging, and grasping. Females respond by skating away or by employing other evasive maneuvers. If males successfully grasp females, then females resist by initiating a premating struggle. Struggles consist of various behaviors, such as rolls and somersaults, and usually result in males being dislodged. Both male harassment and superfluous mating is costly to females (reviewed in Rowe 1994; Rowe et al. 1994; Arnqvist 1997; Watson et al. 1998), and females appear to adjust their resistance to balance the costs imposed by male harassment relative to those of mating. In short, females accept superfluous mating attempts to reduce the costs of further harassment. As such, the mating system of many *Gerris* has been described as one of convenience polyandry (Rowe 1992; Rowe et al. 1994; cf. Thornhill and Alcock 1983).

Ecological studies have demonstrated an inverse relationship between female mating rate (matings per female per hour) and female resistance. If local ecological conditions are altered experimentally to increase the optimal female mating rate, then females reduce their level of resistance (pre-mating struggle duration) and the rate of mating increases (e.g., Arnqvist 1992a; Rowe 1992; Vepsäläinen and Savolainen 1995; Rowe et al. 1996; Ortigosa and Rowe 2002). For example, when costly harassment rate is elevated, females reduce their resistance and thereby increase mating rates. In fact, the characterization of the mating system as convenience polyandry results from a series of experimental studies examining the consequences of shifting the optimal female mating rate (Rowe et al. 1994; Arnqvist 1997).

It is easy to see how optimal female mating rate may vary over evolutionary time. For example, one of the main costs to females of mating is increased predation. If a species evolves antipredator traits or shifts habitat in a manner that reduces the susceptibility to predation during mating, then we would expect the costs of mating to be reduced, and therefore, optimal mating rate to evolve upward. This response would be expected from any evolutionary change affecting the costs of mating to females. If evolutionary change in optimal mating rate of females underlies evolutionary change in the mating system, then we would expect a *negative* association among species between mating rates and pre-

mating struggle duration. Females of species with higher optimal mating rates would be less resistant to mating than those with lower optima, when compared in a common environment. We call this the evolving female optima hypothesis.

In contrast to this ecological view, an intersexual arms race may drive the evolution of mating rate in the absence of ecological change. In water striders, conflict over mating, manifested in the premating struggle, results in selection for grasping traits in males and antigrasping traits in females. Armaments include enlarged forelegs, antennae, and genitalia in males and abdominal spines in females (Rubenstein 1984; Arnqvist 1989a; Arnqvist and Rowe 1995; Preziosi and Fairbairn 1996; Weigensberg and Fairbairn 1996; Westlake et al. 2000). These structures give each sex an advantage over the other in the premating struggle (Arnqvist and Rowe 2002b). Male grasping structures increase the duration that males can withstand female resistance and thereby increase their success at achieving mating. Similarly, antigrasping structures in females increase the speed at which they can repel males in the premating struggle, and thereby reduce their mating frequency. In both cases, high mating rates are associated with long premating struggle durations, reflecting the ability of males to withstand longer struggles. Therefore, interspecific variance in the relative advantage of the sexes would lead to a pattern of covariance in which long premating struggles are associated with high mating frequency. This is the opposite pattern of evolutionary covariance predicted by the evolving female optima hypothesis.

In this paper we combine experimental and comparative approaches to study the coevolutionary dynamics of mating behaviors among 15 species of water striders in the genus *Gerris*. The primary goal of our paper is to test the contrasting predictions from the evolving female optima and antagonistic coevolution hypotheses. We first derive specific predictions, under the two hypotheses, for the expected across-species covariances of a large suite of mating behaviors that collectively make up the mating system. To adequately test these hypotheses, we need to first determine whether all of these species share the convenience polyandry mating system, known from the few well-studied species. We do this by replicating a sex-ratio manipulation, which alters the optimal mating rate of females (Arnqvist 1992a; Rowe 1992; Vepsäläinen and Savolainen 1995) and recording the effects on behavior in each species. Then we test our key interspecific hypotheses with the observed sign of covariances among mating behaviors. To do this, we use the species mean values from this first experiment, supplemented with an experiment designed to quantify interspecific differences in the relative ability of females to repel males.

MATERIALS AND METHODS

Mating Behavior in Gerris

The mating system of water striders includes a number of behavioral components (pre-mating struggles, mating rates, harassment of females, copulation and guarding durations) and emergent properties (variance in mating success) that have been extensively studied within this group using economic and functional approaches (reviewed in Rowe et al. 1994; Arnqvist 1997). Although a few species of *Gerris* have

been well studied (*G. buenoi*, *G. lacustris*, *G. lateralis* and *G. odontogaster*), there is little or no information on most species in the genus. We base our descriptions and predictions on those intensely studied species, but note that one of the goals of our experiments is to determine how much of this behavior is shared in the group.

Single females are frequently harassed by males, but this usually does not lead to mating. Mating commences after a premating struggle of varying duration (see above) and consists of two components: copulation (male is mounted on top of the female with his genitalia inserted in hers) and guarding (male remains mounted on top of the female but without genital contact). Single males do not attempt to displace males during copulation or guarding. Copulation is terminated when the male withdraws his genitalia, and there is no evidence that the female influences this duration (Rowe 1992; Vepsäläinen and Savolainen 1995; Rowe and Arnqvist 1996; Arnqvist and Danielsson 1999; Danielsson 2001). In contrast, the guarding phase is usually terminated with a struggle initiated by females, and females appear to have primary influence over the timing and success of this struggle (Rowe 1992; Vepsäläinen and Savolainen 1995). In at least one species, males may also affect this duration (Jablonski and Vepsäläinen 1995; Vepsäläinen and Savolainen 1995).

Background Experimental Conditions

We used two types of experiments on adult water striders. The first was designed to yield species-level data for a variety of mating components and to quantify the effects of sex ratio on these variables. The second was designed to yield species-level data on harassment and mating attempts. Each experiment consists of 15 subexperiments, each conducted independently with one of the species. We made every possible effort to standardize biotic and abiotic protocol under which these subexperiments were conducted. Experiments were conducted in Albuquerque (NM, USA), Toronto (Ontario, Canada), and Umeå (Sweden).

Focal species and their collection sites are given in a companion paper (Arnqvist and Rowe 2002a). These species share a similar ecology and life history, and the phylogeny of the group is well supported (Andersen 1982, 1993; Damgaard and Sperling 2001). Each species was collected from their home site one to five days prior to the experiments and was in full reproductive condition. During this period, individuals were held in stock pools in the laboratory at sex ratios near 1:1, with abundant food (frozen fruitflies and crickets) and aeration. Laboratory air temperature was $20 \pm 2^\circ\text{C}$. Pools in which experiments were conducted had a surface area of 2400 cm² and a depth of 3–6 cm and were equipped with two small floating islands for resting (Styrofoam strips; $0.2 \times 2.4 \times 2.4$ cm).

Experiment 1: Effects of Sex Ratio

For each species, eight uniquely marked individuals (paint spots on the pronotum and/or midleg femur) were transferred into each of 14–20 replicate pools, at each of two sex ratios (male:female, 3:5 or 5:3). Individuals were acclimated to these conditions for a period of 24 h at which point the observation period began. For the first 23 h of this acclimation

TABLE 1. The number of pools and total duration of observations (h) per replicate pool for each of the 15 *Gerris* species used in experiments 1 and 2. Because two sex ratios were used in experiment 1, the number of replicates at each sex ratio is half the number of pools shown in the table.

Species	Experiment 1		Experiment 2	
	No. pools	Duration of observations	No. pools	Duration of observations
<i>G. argentatus</i>	18	12.0	6	1.0
<i>G. brasili</i>	20	14.0	10	1.0
<i>G. buenoi</i>	16	15.0	8	1.0
<i>G. comatus</i>	16	13.0	6	1.0
<i>G. gibbifer</i>	20	14.0	10	1.0
<i>G. gillettei</i>	14	9.0	6	1.0
<i>G. incognitus</i>	18	12.5	6	1.0
<i>G. incurvatus</i>	26	13.0	7	1.0
<i>G. lacustris</i>	18	12.0	6	1.0
<i>G. lateralis</i>	18	12.0	7	1.0
<i>G. marginatus</i>	14	12.0	6	1.0
<i>G. odontogaster</i>	18	12.0	6	1.0
<i>G. pinegrensis</i>	16	14.5	7	1.0
<i>G. sphagnetorum</i>	18	20.0	8	1.0
<i>G. thoracicus</i>	18	25.5	6	1.0

period, abundant food and aeration were provided. Observations were conducted over two consecutive days for at least 6 h on each. The number of replicate pools and the total duration of observations for each species are given in Table 1.

Any mating pairs observed immediately prior to the start of the experiment were gently interrupted, and only those pairs that had initiated mating by the end of the experiment were used in our calculations. We continued to observe pairs after the observation period if they had initiated mating during the observation period, so their mating durations could be included in the analysis. At 10-min intervals throughout the experiment, each pool was checked for copulating or guarding pairs and the identity of any mating individuals was recorded. From these data we initially extracted mean values for seven behaviors: (1) mating rate, the number of matings per individual female per hour of observation; (2) copulation duration, male aedeagus inserted; (3) guarding duration, male mounted on female without aedeagus inserted; (4) mating duration, the sum of copulation and guarding durations; (5) mating activity, the proportion of the total observation period that an individual female was mating (i.e., copulating or being guarded); and (6, 7) individual variation in mating rate for both sexes, the coefficient of variation in mating rate among individuals in a given replicate. For each of the seven variables, we retained a species value represented by the mean across all replicates. We also calculated a sex-ratio effect for each of the seven original variables by subtracting the value of a behavior at sex ratio 5:3 from that at 3:5. This yielded a total of 14 behavioral variables for each species.

Predictions for sex-ratio effects

Based on prior experiments with three of the 15 species, we expected that biasing the sex ratio toward males would lead to a decrease in female resistance to mating. The increased density of males increases costly harassment of single females and, thus, increases the net benefits of mating to

females. Consequently, females reduce their resistance to mating, and mating rates and durations are elevated (Arnqvist 1992a; Rowe 1992; Vepsäläinen and Savolainen 1995). Therefore, we predict that biasing the sex ratio toward males in the current experiments will lead to an increase in mating rates, guarding duration and, therefore, mean mating duration and activity. Unlike mating frequency and duration, males control copulation duration (see above); therefore, we do not expect a relationship between optimal female mating rate and copulation duration. Nevertheless, past experiments suggest that males increase copulation duration as the sex ratio becomes more male biased as expected from theories of male-male competition (Rowe 1992; Vepsäläinen and Savolainen 1995).

In *Gerris*, sexual selection by female choice of male morphology (size and grasping structures) results as a pleiotropic effect of female resistance (reviewed in Rowe et al. 1994; Arnqvist 1997). General theory suggests that the opportunity for sexual selection should increase when local sex ratio is male biased, as a result of intensified exploitation and interference competition among males (Wade and Arnold 1980; Andersen 1994). However, in *Gerris*, this effect is at least partly countered by an induced reduction in female resistance, leading to less intense sexual selection by female choice (Arnqvist 1992a,b). Thus, we predict that the positive effects of a male-biased sex ratio on the net opportunity for sexual selection (measured as individual variation in male mating rate) should be less pronounced, or even reversed, in species where females markedly reduce their resistance.

Experiment 2: Harassment and Struggle Duration

Observations were gathered from experimental pools containing eight individuals at a sex ratio of 3:1, where females were marked with a pronotal paint spot to easily distinguish them from males. Females were transferred directly from the stock pools to the experimental pools at the start of the observation period. Males were transferred from the stock pools and individually isolated in glass jars or plastic cups (8-cm diameter), provided with abundant food, for 24 h prior to the start of the observation period. Our experience is that holding males in this way increases their incentive to mate. Continuous observation lasted 1 h per replicate (Table 1).

During these observations, we counted and timed (with a stop watch) all behaviors, so that the following six variables could be calculated: (1) harassment index, where a harassment event is any male-initiated disturbance or interference of females that required some type of avoidance action by females, including anything from lunges and chases to grasping by males; the harassment index expresses the number of harassments a single female experienced on average per minute, assuming the presence of six single males; (2) unsuccessful struggle duration, defined as the average time required for females to dislodge males following a mating attempt; we define mating attempts as those harassment events that resulted in males being aligned on top of females, in mating position; (3) Successful struggle duration, defined as the duration of struggles that actually led to mating; and (4–6) three linked indices of the relative success of male effort, the proportion of harassment events resulting in premating struggles,

the proportion of harassment events resulting in mating, and the proportion of premating struggles that led to mating.

Interspecific predictions for the covariances among mating behaviors

If differences among species can be accounted for by evolved differences in optimal female mating rate (the evolving female optima hypothesis), then we would expect species to fall along an axis similar to that which connects mating behaviors from female-biased conditions to increasingly male-biased conditions. At one end, analogous to female-biased sex ratios, would be species characterized by low optimal female mating rates, and at the other, analogous to male-biased sex ratios, high optimal female rates. In species that have low optimal rates, we would expect high female resistance leading to long premating struggles, with a lower proportion leading to mating and reduced mating frequency and guarding duration. This would lead to reduced total mating durations and activity. We cannot specify an effect on copulation duration or the rate at which males harass females, because females do not appear to influence these variables.

In contrast, under the antagonistic coevolution hypothesis, we expect the opposite pattern to that described above. Under this hypothesis, variation in mating behavior is attributable to evolved differences in the relative ability of the sexes to prevail in struggles. Longer premating struggles would reflect an evolved advantage in males to withstand female resistance, whereas short struggles would reflect an evolved advantage in females to dislodge males during the struggle. This should lead to longer struggles, more often leading to mating and thereby to an increased mating frequency at the male-advantage end and the opposite at the female-advantage end. At the male-advantage end, there may also be longer guarding durations for two reasons. First, females may delay terminating matings as the costs of rejecting subsequent males are elevated. Second, if guarding duration is determined, in part, by a male's ability to withstand postmating struggles, the increased relative ability of males would result in longer guarding durations in these species. Increases in mating frequency and guarding duration are expected to increase total mating duration and mating activity. An increased relative ability of males to overcome female resistance should also be associated with low opportunity for sexual selection.

Phylogeny and comparative analysis

The phylogeny on which we test for pattern in the coevolution of behaviors is the total evidence hypothesis of Damgaard and Sperling (2001), and is shown in Figure 1. Note that the placement of two species, *G. incurvatus* and *G. brasili* (not included by Damgaard and Sperling 2001), is based on morphology alone (J. Damgaard and N. M. Andersen, pers. comm.). We employed standard comparative methods to test for correlated evolution (Felsenstein 1985; Harvey and Pagel 1991; Garland et al. 1992; Price 1997; Martins 2000) and computed phylogenetically independent contrasts using the Contrast module of PHYLIP (available via <http://evolution.genetics.washington.edu/phylip.html>). No branch lengths have been estimated for our hypothesis, so we assumed equal

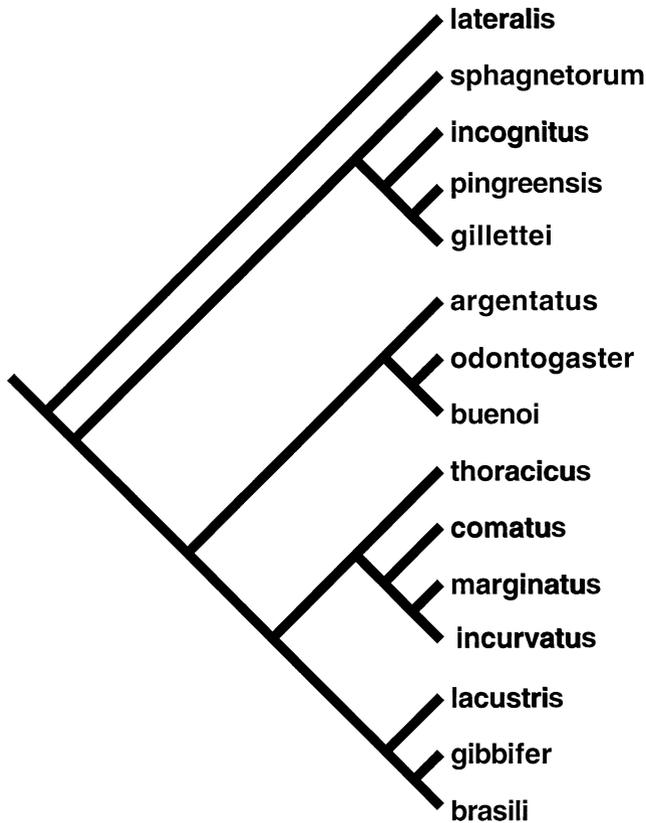


FIG. 1. The phylogenetic hypothesis used in this analysis. We show only those *Gerris* species included in our study, but the hypothesis is based on molecular and morphological analyses of 28 species from four genera (see Damgaard and Sperlberg (2001)).

branch lengths in our analysis (Harvey and Pagel 1991; Martins and Garland 1991).

RESULTS

Experiment 1: Effects of Sex Ratio and Species on Mating Behavior

We initially analysed behavioral traits from experiment 1 with two-way ANOVA, where data were represented as single means from a given pool. Therefore, pools ($N = 268$) were our unit of replication rather than individuals ($N = 2144$). We use these analyses (see Table 2) to determine, first, whether species differ significantly in their mating behavior, and second, whether previous results of shifting optimal female mating rate by sex-ratio manipulation are indeed generalized.

Species vary in the magnitude of mating behaviors, and the range in values among species is dramatic. For all behaviors, the species term in the ANOVA was highly significant and large in magnitude, with differences in species means ranging from a factor of three (copulation duration, CVs of male and female mating rates) to over an order of magnitude (female mating rate and activity). For example, mean female mating activity in female-biased sex ratios ranged from 1% in *G. sphagnetorum* to 75% in *G. lateralis*.

Sex ratio was also a consistently significant factor in our analyses (Table 2). However, because of significant inter-

actions between sex ratio and species, interpretation is difficult. To better understand these interactions, we plot and analyze the relationship between species trait values expressed in the female-biased sex ratios with those in the male-biased sex ratio. Note that this analysis is meant to facilitate our understanding of these sex ratio \times species interactions, not to test the sex-ratio effect itself. Indeed, this analysis is considerably less powerful in detecting overall sex-ratio effects, as the unit of analysis is species ($N = 15$), rather than pool ($N = 268$) used in the initial analyses. Plots and subsequent regression analyses reveal two clear patterns in the dataset, which generally support our predictions and can account for the nearly ubiquitous sex ratio \times species effects seen in the initial analyses (Fig. 2). First, the responses to sex ratio were usually in the directions we had predicted (see above). Guarding duration, mating duration, rate, and activity all tended to have higher values in male, compared to female-biased sex ratios (Fig. 2). This effect is significant as indicated in the initial analysis (sex-ratio effect in Table 2). Note that most points fall above the 1:1 line, which connects the values predicted if behaviors were unaffected by sex ratio. Second, in these traits, the response to sex ratio was greatest in those species that had the highest value in the female-biased sex ratio. This is indicated by observed regressions slopes that are significantly greater than 1.0 (Fig. 2) and is the source of the significant interaction terms in the initial analyses (Table 2). To determine whether increased values in the male-biased treatments were simply proportional to those in the female-biased treatment, we reanalyzed the data by adding a quadratic term into the regression. The addition of a quadratic term significantly improved the regression model only for female mating rate ($t = 1.158$, $P = 0.016$), where it was negative, indicating that the response to sex ratio was somewhat less than proportional for this behavior.

Copulation duration increased in the male-biased treatment (Table 2, Fig. 2), but this difference was not an increasing function of the value expressed in the female-biased treatment. Finally, female mating rate CV decreased and male mating rate CV increased overall in the male-biased treatment.

Experiment 2: Effects of Species on Harassment and Struggle Duration

To assess differences between species, the results of experiment 2 were subjected to one-way ANOVA in which data were represented as single means from a given pool. Therefore, pools ($N = 115$) were our unit of replication rather than individuals ($N = 920$). All behavioral traits measured in these experiments varied dramatically between species, with differences in species means spanning one to two orders of magnitude (see Table 3). Most notably, the average duration of pre-mating struggles varied from a few seconds to several minutes and the average probability of a struggle ending with mating varied from near zero to 0.83. Across all replicates, the average duration of struggles leading to mating was significantly longer than was that of struggles ending with male dislodgement ($N = 44$; paired t -test, $t = 2.31$, $P = 0.026$; Wilcoxon signed ranks test, $Z = 2.031$, $P = 0.042$).

TABLE 2. Effects of species, sex ratio, and their interaction for each of the behavioral variables from experiment 1 (see Materials and Methods for definitions). Summary statistics are for individual ANOVA for each behavior.

Behavioral variable	Factor		
	Species (df = 14)	Sex ratio (df = 1)	Sex ratio × species (df = 14)
Copulation duration ¹	$F = 21.706$ $P = 0.000$	$F = 12.258$ $P = 0.001$	$F = 3.936$ $P = 0.000$
Guarding duration ¹	$F = 17.680$ $P < 0.001$	$F = 19.006$ $P < 0.001$	$F = 2.517$ $P < 0.002$
mating duration ¹	$F = 21.012$ $P = 0.000$	$F = 26.724$ $P = 0.001$	$F = 2.738$ $P = 0.001$
Female mating rate ²	$F = 33.074$ $P < 0.001$	$F = 67.926$ $P < 0.001$	$F = 2.815$ $P = 0.001$
Female activity ²	$F = 67.978$ $P < 0.001$	$F = 122.692$ $P < 0.000$	$F = 7.653$ $P < 0.001$
CV male mating rate ¹	$F = 17.868$ $P = 0.000$	$F = 4.000$ $P = 0.047$	$F = 1.272$ $P = 0.226$
CV female mating rate ¹	$F = 11.893$ $P < 0.001$	$F = 55.334$ $P < 0.001$	$F = 1.794$ $P = 0.040$

¹ Error df = 229.² Error df = 240.

Correlations between behavioral traits across species

Our main hypothesis requires an understanding of the pattern of coevolution of the various behavioral components of the mating system. To characterize variation in mating system across species and to reduce the dimensionality of behavioral variation, we subjected our behavioral data to a principal components analysis (PCA). This analysis was run on the correlation matrix and the components were not rotated. We analyzed two classes of data jointly: mean species values (from experiments 1 and 2) and the responses of each species to the sex-ratio manipulation (experiment 1). We did not include the duration of successful struggles in this analysis because of missing values for five species, but subsequently calculated the loading (Pearson correlation coefficient) of this behavior on each principal component (PC) from the remaining 10 species.

We applied the broken-stick model as a stopping rule (see Jackson 1993), which yielded three PCs. Each PC accounted for more than 10% and collectively for almost 80% of the variance in the total dataset. The eigenvalues (λ values) for these components were 9.65, 2.92, and 2.14, respectively. Loadings on these multivariate dimensions are shown in Table 4, and the ordination of the various species along PC1 and PC2 are shown in Figure 3. The first axis accounts for 50.8% of the variance in behavior across species, and most of the species-level traits load heavily and significantly on it (see Table 4). We interpret this axis as one describing how species vary in the magnitude of these tightly covarying behaviors. Specifically, struggle duration (unsuccessful and successful), the various measures of success of these struggles, and female mating activity and most of those components that constitute it load heavily on this axis. Species with high PC1 scores can be characterized as having long pre-mating struggles, which are likely to lead to mating and consequently to high mating rates and durations. High PC1 scores are also associated with reduced individual variation in mating rate (CVs). The negative loading of male mating rate CV shows that the opportunity for sexual selection is lower in

species where males are relatively efficient at converting pre-mating struggles into matings. Harassment rate and copulation durations had the lowest loadings on this axis.

PC1 also captures the sign and magnitude of the species' sex-ratio response because these responses were typically proportional to the magnitude of species averages (see Fig. 2). One striking exception is the effects of sex ratio on male mating rate CV. As expected, our sex-ratio treatment had a relatively small effect on the opportunity for sexual selection in species where females alter their behavior greatly in response to sex ratio. For example, compare the sign of the loading for sex ratio/female mating activity (0.942) with that of sex ratio/male mating rate CV (-0.478), which is an index of sexual selection (Table 4). Notably, several of our variables (e.g., mating duration, mating activity) are sums or products of others. When these variables were dropped from the analysis, neither the sign nor the significance of the remaining variables changed.

PC2 and PC3 account for a relatively small proportion (15.4% and 11.3%) of the total variance in the dataset. PC2 primarily captures two species characteristics (Table 4). First, males of species with a low score on PC2 frequently harass females but are inefficient at converting these harassments into mating. Second, the proportional increase in female mating rate as a result of a male-biased sex ratio is high among females of species with a low score on PC2, and individual variation in mating rates simultaneously decrease, presumably as a result of a larger proportion of individuals mating. Males of species with a high score on PC3 tend to exhibit long average copulation durations and have particularly prolonged copulations in response to male-biased sex ratios.

Correlated evolution of behavioral traits

Ultimately, if we wish to understand the evolutionary covariation among behaviors, we need to account for any phylogenetic effect in the dataset. However, studying correlated evolution across multiple traits presents special problems. In particular, third variables may confound coevolution between

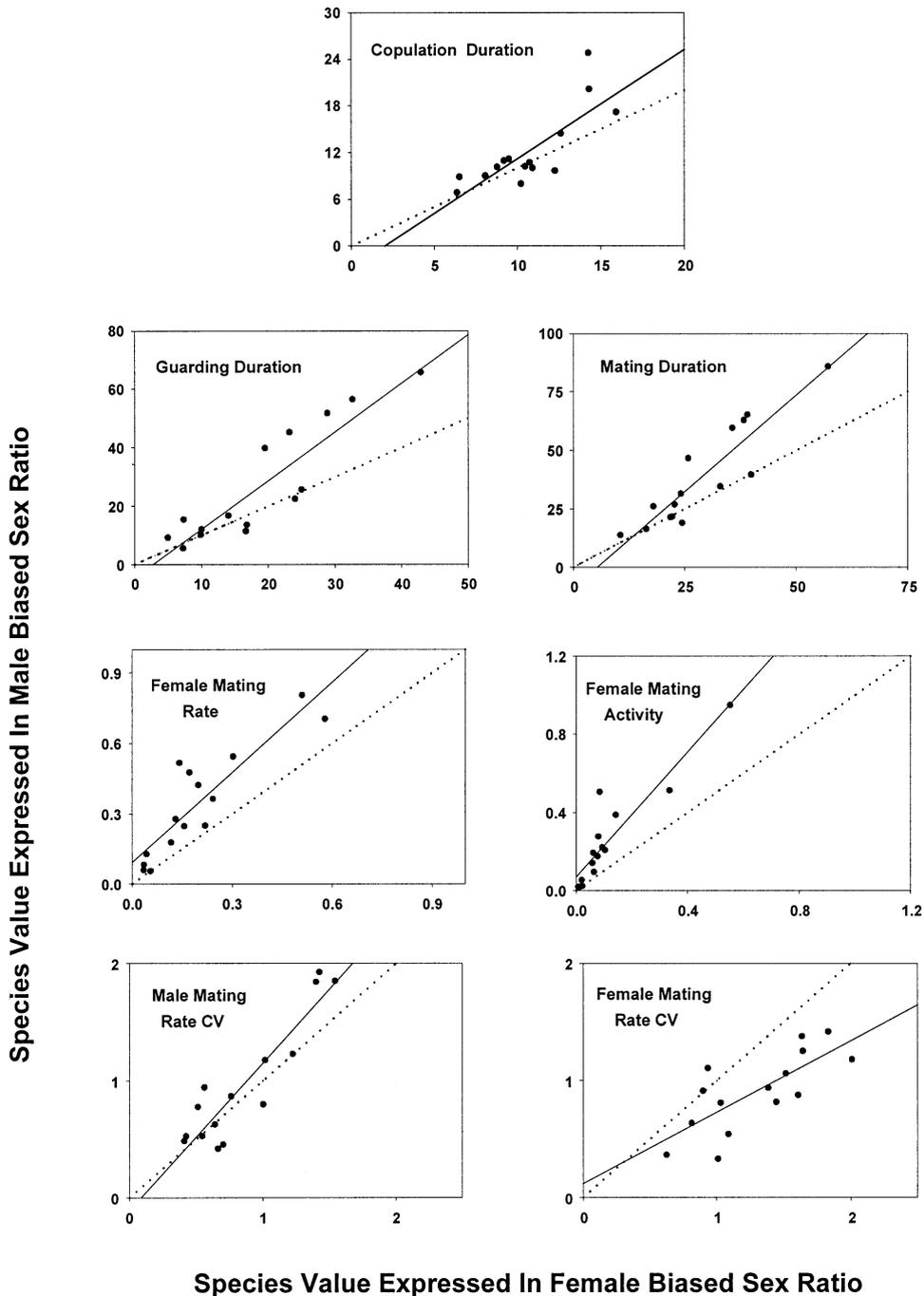


FIG. 2. The relationship between behavioral trait values in female-biased and male-biased sex ratios. Each point represents a species value calculated from experiment 1. The dashed line in each panel has a slope of one and passes through the origin. It represents the expected relationship under the null hypothesis of no difference in behavior in male-biased and female-biased sex ratios.

pairs of focal traits (Price 1997). To study coevolutionary pattern, we therefore applied a multivariate approach rather than focussing on correlated evolution of all possible pairs of traits. First, we reanalyzed our data with a new PCA, using phylogenetically independent contrasts for each behavior rather than species values (Clobert et al. 1998). This analysis generated three evolutionary PCs, which accounted for 53.9%, 14.6%, and 9.6% of the total variation (Table 5). The

eigenvalues (λ values) for these components were 10.24, 2.78, and 1.82, respectively. These evolutionary PCs are clearly very similar to the species level PCs (cf. Tables 4 and 5). All variables on PC1 have similar loadings, and only a few have changed substantially on PC2 and PC3. The overall correlation of variable loadings between the three sets of paired PCs was remarkably high ($r = 0.993$, $r = 0.908$, and $r = 0.749$, respectively). Second, to insure that these patterns

TABLE 3. Species differences in harassment and struggle duration observed in experiment 2 (six males and two females per trial). Ranges are means for each of 15 species. One-way ANOVA tests the effect of species on each of the behavioral variables (see Materials and Methods for definitions).

Behavior	Range	F-value	P
Harassment index	0.03–4.89	$F_{14,90} = 53.09$	<0.001
Struggles/harassment	0.05–0.55	$F_{14,87} = 13.39$	<0.001
Mating/harassment	0.00–0.48	$F_{14,87} = 15.60$	<0.001
Matings/struggle	0.00–0.83	$F_{14,72} = 13.24$	<0.001
Unsuccessful struggle duration (sec)	2.19–20.87	$F_{14,68} = 11.75$	<0.001
Successful struggle duration (sec)	3.80–157.70	$F_{9,38} = 10.52$	<0.001

were robust, we bootstrapped (1000 replicates) both the species level PCs and the evolutionary PCs and correlated the median loading of all variables (Jackson 1993). Again, the overall correlation between the median loadings of the three sets of paired PCs was remarkably high ($r = 0.994$, $r = 0.938$, and $r = 0.718$, respectively). Third, we computed independent contrasts for the original species level PCs (Table 4) and correlated these with the corresponding PC scores of the evolutionary PCs. The correlations among the three sets of paired variables were, again, very high ($r = 0.999$, $r = 0.932$, and $r = 0.771$, respectively). Collectively, these analyses strongly suggest that behaviors coevolve in a concerted fashion along these multivariate dimensions.

As predicted by the antagonistic coevolution hypothesis, we found that mating rate and activity increased, rather than decreased, with increasing struggle duration (Fig. 4). In these regression analyses, regressions were forced through the origin (Garland et al. 1992). Specifically, mean mating rate of females ($R^2 = 0.438$, $P = 0.004$) and mating activity ($R^2 = 0.485$, $P = 0.004$) were significantly increasing functions of struggle duration. Guarding duration approached significance

($R^2 = 0.230$, $P = 0.040$), but was highly influenced by an outlier (Fig. 4). When this contrast was removed, the regression was highly significant ($R^2 = 0.698$, $P < 0.001$). These coevolutionary patterns were the opposite of those predicted by the evolving female optima hypothesis. We had no predictions for copulation duration, and it was not significantly related to struggle duration ($R^2 = 0.166$, $P = 0.131$).

Evolutionary trends or random walk

Using a punctuational model, which assumes that evolutionary change occurs during speciation events, we assessed coevolutionary trend by correlating the number of past speciation events (i.e., nodes) during each species evolutionary history with its current mating system state (reflected in PC1, PC2, and PC3, values). If there were some consistent direction to evolution, then we would expect significant correlation coefficients. However, the number of estimated past speciation events did not correlate significantly with current mating system across species (Spearman rank correlations; PC1: $r = -0.169$, $P = 0.547$; PC2: $r = -0.450$, $P = 0.092$; PC3: $r = 0.217$, $P = 0.437$).

TABLE 4. Principal components analysis of mating behavior from 15 species of *Gerris*. The bottom seven (sex-ratio) variables were calculated as the difference in each behavior when tested at two sex ratios (see Materials and Methods). Collectively, the three principal components explain over 77% of the variance in the total dataset (50.77%, 15.37%, and 11.26%, respectively). Tests of significance of variable loadings represent frequency of loadings different in sign to the ones observed, among 100 bootstrap replicate analyses corrected for axis reversals (Mehlman et al. 1995).

Behaviors	Component loadings		
	1	2	3
Unsuccessful struggle duration	0.799*	-0.181	-0.046
Successful struggle duration [†]	0.733	0.413	0.297
Harassment index	0.287†	-0.625†	0.273
Success/harassment	0.760*	0.326†	0.318
Success/struggle	0.788*	0.235	0.421
Struggles/harassment	0.611*	0.160	-0.390
Copulation duration	0.343	-0.089	0.789*
Guarding duration	0.891*	0.286†	-0.215
Mating duration	0.939*	0.217*	-0.027
Female mating rate	0.800*	-0.425†	0.309
Female mating activity	0.934*	-0.011	0.264
Male mating rate CV	-0.772*	0.332†	-0.036
Female mating rate CV	-0.842*	-0.066	0.031
Sex ratio: copulation duration	0.411†	0.297	0.485†
Sex ratio: guarding duration	0.745*	0.303	-0.483
Sex ratio: mating duration	0.785*	0.378†	-0.354
Sex ratio: female mating rate	0.469*	-0.805*	-0.233
Sex ratio: female mating activity	0.942*	-0.076	-0.231
Sex ratio: male mating rate CV	-0.478*	0.665†	0.299
Sex ratio: female mating rate CV	0.047	0.677†	0.058

† $P < 0.15$, * $P < 0.05$.

[†] Variable not included in the principal components analysis due to missing data. Loadings represent correlation between variable and principal component.

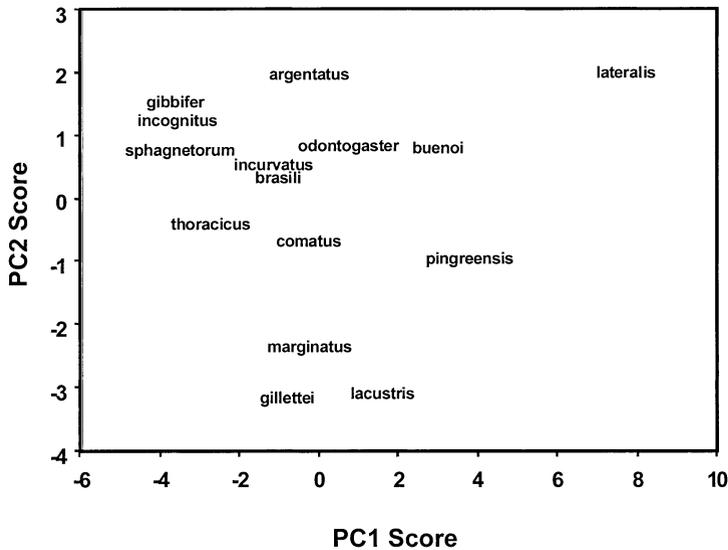


FIG. 3. Ordination of the 15 *Gerris* species studied along the first two principal components from a principal components analysis based on extant species data (see Table 4 and Materials and Methods section).

DISCUSSION

Although water striders have been recognized as model group for studies of sexual conflict, prior to this study our understanding of the mating system was primarily limited to a small subset of within-species studies. Comparative studies of mating behaviors within this group have been conducted before, but these were limited to mapping discrete and rather arbitrary transitions between mating system classes (e.g., Andersen 1997) or describing patterns of sexual selection across species (e.g., Fairbairn 1988; Arnqvist et al. 1996; Rowe and

Arnqvist 1996). Here we aimed to describe the coevolutionary pattern of those behaviors that make up the mating system and distinguish the processes that underlie this pattern. We address four main points. First, despite more than an order of magnitude range among species in some behaviors and their response to sex ratio, these species can be said to share a common mating system. Second, evolution within this mating system results to a large degree from antagonistic coevolution over mating rate. Third, the pathway of this coevolution seems to regularly change sign. Finally, we use these data to illustrate some of the pitfalls resulting from classifying mating systems into male or female advantage or male or female win.

The Evolutionary Covariance of Behaviors within a Shared Mating System

The mating system of the few previously studied species has been described as one of convenience polyandry (Rowe 1992; Rowe et al. 1994; Vepsäläinen and Savolainen 1995; Arnqvist 1997). Mating is costly to females, but so is sexual harassment suffered when not mating (Rowe 1994; Watson et al. 1998). Females resist harassing males with a struggle and adjust this resistance in accord with variation in their optimal mating rate. Mating behaviors of the much larger set of species studied here corresponds to that described for the few previously studied species. Moreover, behaviors of each species responded qualitatively similarly to our experimental manipulation of sex ratio, and consequently optimal mating rates of females. Thus, we conclude that all species included in our study share the convenience polyandry mating system. Several studies of other systems suggest that convenience polyandry is much more widely distributed both among insects (e.g., Thornhill and Alcock 1983; Rehfeldt 1996; Choe and Crespi 1997; Clutton-Brock and Langley 1997; Crean et

TABLE 5. Principal components analysis for *Gerris* mating behavior using phylogenetically independent contrasts. See Table 4 and Materials and Methods for more details. Collectively, the three principal components explain 78% of the variance in the total dataset (53.91%, 14.64%, and 9.57%, respectively). Tests of significance of variable loadings represent frequency of loadings different in sign to the ones observed, among 1000 bootstrap replicate analyses corrected for axis reversals (Mehlman et al. 1995).

Behaviors	Component loadings		
	1	2	3
Unsuccessful struggle duration	0.724*	-0.283	0.328
Harassment index	0.371†	-0.529	0.266
Success/harassment	0.747*	0.114	0.528*
Success/struggle	0.807*	0.010	0.526†
Struggles/harassment	0.701*	0.440†	-0.136
Copulation duration	0.407†	-0.452†	0.309
Guarding duration	0.838*	0.401†	-0.030
Mating duration	0.918*	0.253†	0.052
Female mating rate	0.800*	-0.522†	0.100
Female mating activity	0.944*	-0.173	0.231
Male mating rate CV	-0.878*	0.146	0.104
Female mating rate CV	-0.853*	-0.265†	0.047
Sex ratio: copulation duration	0.516†	0.318	0.038
Sex ratio: guarding duration	0.779*	0.334	-0.406
Sex ratio: mating duration	0.796*	0.407	-0.328
Sex ratio: female mating rate	0.637*	-0.575*	-0.425
Sex ratio: female mating activity	0.955*	0.030	-0.261
Sex ratio: male mating rate CV	-0.559*	0.499*	0.500
Sex ratio: female mating rate CV	-0.050	0.658*	0.344

† $P < 0.15$, * $P < 0.05$.

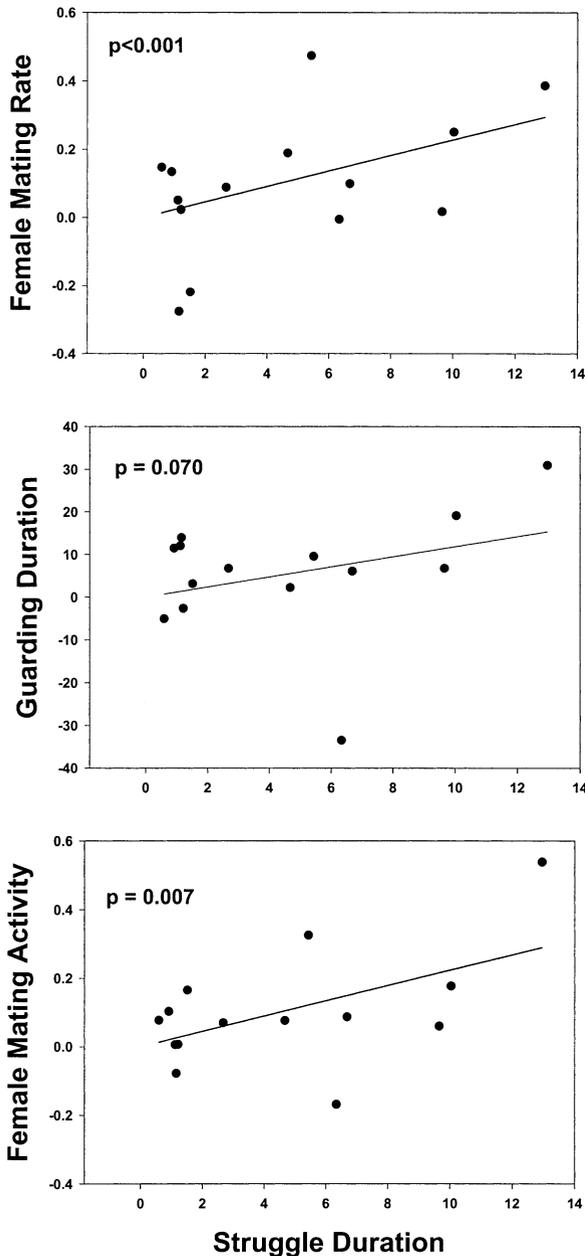


FIG. 4. The evolutionary correlations between struggle duration (unsuccessful) and guarding duration, female mating rate, and female mating activity. Data represent independent contrasts (see Materials and Methods section). Successful and unsuccessful struggle durations are closely correlated (see Table 4), but we use unsuccessful struggles because the dataset for successful struggles is incomplete (see above).

al. 2000) and other animals (e.g., Magurran and Seghers 1994; Byrne and Roberts 2000; Galimberti et al. 2000; Shine et al. 2000) than was previously thought.

Despite this qualitative similarity among species, we found substantial quantitative variation among species in the magnitudes of each behavior (e.g., mating rate, guarding duration) and their responses to sex ratio. However, PCAs revealed that a large portion of this interspecific variation (> 50%) could be accounted for with a single multivariate dimension

(Table 4, Fig. 3), suggesting that the magnitude of each behavior and its response to sex ratio tightly covaries among species. When our data was reanalyzed using phylogenetically independent contrasts, a covariance pattern virtually identical to the species-level pattern appeared (Tables 4, 5). We conclude that the evolution of these behaviors is constrained to a defined trajectory by a set of tight covariances among behaviors. Some of the behaviors that we have analyzed are bound to covary, but others are not. For example, mating activity is a product of mating rate and mating duration and all three covary positively with our PC1. It follows, from the calculation of mating activity, that both mating rate and mating duration would covary with mating activity. However, it does not likewise follow that mating rate and mating duration necessarily covary.

We wish to emphasize those central elements of the within-species dynamics of this mating system that may account for the cohesive evolution of mating behaviors. Interactions between the sexes are characterized by a fairly simple conflict over mating rate and duration (see Rowe et al. 1994; Arnqvist 1997), the overt manifestations of which are pre and post-mating struggles. Both mating rates and durations are outcomes of these struggles. If indeed these major components of mating are determined in such a simple fashion, then only two coevolutionary patterns are possible: either an association between *short* struggles (reduced mean female resistance) and high mating activity or between *long* struggles (increased ability of males to overcome struggles) and high mating activity. Notably, sexual selection on males for size and clasping traits and natural selection on females for anticlasping traits are also linked directly to premating struggles (Arnqvist 1989a, 1992b,c; Arnqvist and Rowe 1995). Thus, this simple conflict between the sexes over mating in *Gerris* might constrain their key mating behaviors and associated morphologies to a limited number of evolutionary pathways. Similar conflicts over mating appear characteristic of other water strider genera (e.g., *Aquarius*, Sih and Krupa 1992; Weigensberg and Fairbairn 1994; Lauer 1996), as well as many other taxa (e.g., Magurran and Seghers 1994; Clutton-Brock and Parker 1995; Rehfeldt 1996; Clutton-Brock and Langley 1997; Arnqvist and Nilsson 2000; Byrne and Roberts 2000; Crean et al. 2000; Galimberti et al. 2000; Shine et al. 2000), and may similarly constrain mating-system evolution to a relatively small number of trajectories. Only comparative studies of clades, for which experimental studies have elucidated the dynamics of the conflict over mating, can address this proposition.

Evolution of Optimal Female Mating Rate or Antagonistic Coevolution

The primary motivation for this research was to contrast two hypotheses for mating system evolution in the group, which make opposing predictions for the pattern of evolutionary covariance among behaviors. The first hypothesis attributes interspecific variation solely to evolving optima for female mating rate. This hypothesis derives from known phenotypic responses to experimentally altered female optima (reviewed in Rowe et al. 1994; Arnqvist 1997) and corresponds to a traditional ecological view of mating systems

and their evolution (Emlen and Oring 1977; Vehrencamp and Bradbury 1984; Davies 1991; Arnold and Duvall 1994). The evolving female optima hypothesis predicts that in species where the optima is high, females will reduce resistance to mating, leading to shorter premating struggles and, as a result, increased mating frequency and duration. Our experimental manipulation of optimal mating frequency (sex ratio) demonstrated that behaviors *within* species appear to respond in just such a way. However, the *among-species* covariation in struggle duration and these elements of mating was just the opposite. Species with long struggle durations exhibited high mating frequencies, durations, and overall mating activity. We conclude that the evolving female optima hypothesis can be rejected.

The second hypothesis (antagonistic coevolution) attributes interspecific variation within the mating system solely to variation in the relative advantage of the sexes in determining the outcome of mating struggles. In species in which males have gained an advantage in withstanding female resistance, struggles will be longer and more likely to lead to mating. In contrast, where females have gained an advantage in resisting males, it will take little time to repel a male. The observed pattern of correlated evolution corresponds precisely to these predictions. Species characterized by long struggles also have high mating rates and durations. Thus, we conclude that species can be arrayed along an axis of relative advantage in determining the outcome of premating struggles (Table 4, Fig. 3). Our analyses of phylogenetically independent contrasts suggest that this axis is the coevolutionary trajectory along which species' behavior evolves. Our antagonistic coevolution hypothesis presumes that species evolve structures or physiological traits that can yield some advantage in struggles. Such male and female structural traits have been well studied in *Gerris* (Arnqvist 1989a, 1992b, 1997; Arnqvist and Rowe 1995), and we show in a companion paper that there is continuous variation in the expression of such traits among these species (Arnqvist and Rowe 2002a). Finally, concurrent research demonstrates that in species in which such male traits are overexpressed relative to females, struggles are long and often lead to mating, as would be predicted by our antagonistic coevolution hypothesis (Arnqvist and Rowe 2002b).

We wish to emphasize that mating rate is perhaps the trait over which the interests of the sexes most generally differ, and this interaction has been the focus of numerous studies (Parker 1979; Choe and Crespi 1997; Holland and Rice 1998; Partridge and Hurst 1998; Arnqvist et al. 2000). Yet, we have very little information on the evolutionary dynamics of mating rate, let alone the cause of that evolution. Some comparative studies focused on the cause of interspecific variance in mating rate (e.g., Webster 1992; Bissoondath and Wiklund 1995; Petrie et al. 1998), but more often they are directed toward the consequences of discrete changes (e.g., monogamy to polyandry) for the evolution of reproductive traits (e.g., Arnqvist 1998; Møller 1998). Our study points to a clear role for sexual conflict in generating interspecific variance in mating rates.

Interestingly, one of the effects we observed of increased male advantage in overcoming female resistance is a decline in the CV of male mating rate (Table 5). Thus, when the

relative advantage for males increases over evolutionary time, the opportunity for sexual selection on additional increases in male adaptations declines. This may put a brake on the process, allowing females to regain some advantage, and may partially explain the general lack of escalation of male (or female) advantage that we see as species move along the evolutionary trajectory of PC1. Parker (1979, 1983a) notes that such changes in the selective regime, induced by achieving advantage in a conflict, are critical to the cyclic evolutionary chases observed in theory (see also Härdling 1999). This process may be a common, and as yet empirically unexplored, element of the dynamics of sexual antagonistic coevolution; as the relative advantage of sex A over sex B increases, selection for further escalation/advantage in sex A declines.

Optimal Male Mating Rate?

Experimental studies of water strider mating systems have focused intensely on female interests (see Mating Behavior in *Gerris*), and it is on this foundation that one of our hypotheses rests (evolving female optima). However, an alternative hypothesis, which we have not yet addressed, is that the pattern of behavioral covariation among species is driven by variation in male interests as would be reflected by optimal male mating rate. It may be that species could be set on an axis where those at one end are characterized by high optimal male mating rates leading to more effort by males, and the opposite at the other end. The expected effect of increasing male effort would include longer premating struggles and possibly higher mating rates. This pattern of covariance is in accord with our data (Tables 4, 5, PC1). However, there is little evidence to be found in past studies supporting such a view, and most direct evidence in the current dataset is contrary. First, optimal mating rates of individual males are always expected to be very high relative to females. Thus, we might expect male mating effort to be high and rather constant. As expected, there is no evidence that experimental manipulation of local ecological conditions or individual state of male water striders has any effect on their effort to mate (e.g., Rowe 1992; Vepsäläinen and Savolainen 1995; Rowe et al. 1996). Second, the two behaviors that should most closely reflect male effort in mating, as they are controlled by males, are harassment rate and copulation duration. Notably, these are the only two species-level behaviors that did not load significantly on PC1, whether calculated from species means or evolutionary contrasts (Tables 4, 5). Similarly, there was no significant evolutionary correlation between copulation duration and struggle duration. We therefore conclude that the major axis of interspecific behavioral covariation is not attributable to interspecific variation in male optimal mating rates.

The major axis of behavioral evolution (PC1) that we have focused on here in some sense reflects a line of antagonistically coevolving abilities in the conflict over mating. Had the dynamics of this coevolution been exactly balanced between the sexes, then no change in relative advantage of one sex over the other would have arisen. In the absence of such change, we would expect little variance in either the struggle duration or the resulting frequency and duration of mating.

It is this sort of balanced coevolution that led Rice (1998, 2000) to caution that the footprints of sexually antagonistic coevolution may be obscured by the process itself. Indeed, in a companion paper, we argue that the evolution of a suite of sexually antagonistic morphological traits is largely accounted for by such a cycle of adaptation and counter-adaptation (Arnqvist and Rowe 2002a). Nonetheless, the substantial interspecific variation in premating struggles we found in behavioral traits along PC1 suggests that perfectly matched coevolution of sexually antagonist traits is not the rule (see also Parker 1979, 1983b; Härdling 1999). We argue that it is these imbalances that are manifested in evolutionary change of the mating system (Arnqvist and Rowe 2002b). Our results are thus also in accord with some models suggesting that male persistence and female resistance may rarely, if ever, reach equilibrium conditions when involved in coevolutionary chases (Arak and Enquist 1993, 1995).

Directionality in the Pattern of Coevolution?

Theory predicts that antagonistically coevolving traits will together escalate, deescalate, or occasionally destabilize. Which of the routes coevolution takes depends on details of the environment, marginal costs and benefits of increments of adaptation, and constraints operating on adaptation in both sexes (Parker 1979, 1983a,b; Arak and Enquist 1993, 1995; Härdling 1999; Gavrillets et al. 2001). Thus, there is no general expectation of escalation during an arms race. Likewise, there is no general evolutionary direction expected in the deviation of species toward male or female advantage. In accord with this theory, we found no pattern to the direction of evolution toward advantage in either sex. Although evolution along this axis was clearly very large in magnitude, the direction of this evolution appears to be random. This is indicated both by the lack of an association between number of past speciation events and mating behaviors of extant species and by the general lack of a phylogenetic effect on mating-system evolution. The lack of such a phylogenetic effect is perhaps most clearly illustrated by the high correspondence between the correlation matrices of behaviors when calculated from species or contrast values (Tables 4, 5).

Advantage to One Sex and Winning or Losing a Conflict

Throughout this paper, we have referred to the relative "advantage" of one sex over the other in the conflict over mating. We believe this can be a useful concept when confined to a tightly delineated interaction, but much less so when used more broadly to classify species. This caution also applies to the concept of one sex "winning" over the other as an outcome of sexually antagonistic coevolution (e.g., Parker 1979; Holland and Rice 1998). Getty (1999) pointed out that the concept that one sex could win over the other lacks precision because, in the vast majority of circumstances, the average fitness of the two sexes will be equal. In the specific case of water striders, it is difficult to imagine one sex generally winning over the other. The observations that males are frequently unsuccessful in translating harassment into mating and that females generally resist all mating attempts indicate that both sexes have been kept off their optimal mating rate by the actions of the other. As a general

outcome of interactions between the sexes, this is in accord with both intuition and recent theory (Gavrillets et al. 2001). Despite this caution, we have found it useful to use the term relative advantage in the struggle (notably without reference to relative fitness of the sexes), without any implication that one sex has somehow won over the other. Our analysis suggests that the relative advantage of the sexes, in this narrowly defined interaction, shifts and wobbles without a consistent direction through evolutionary time. It is this variation in "advantage" that accounts for much of the variation in the mating system of this group.

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