8 • The evolution of water strider mating systems: causes and consequences of sexual conflicts

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ABSTRACT

Water striders (Heteroptera: Gerridae) exhibit two different types of mating behavior. The most common mating system (type I) is characterized by strong apparent conflicts of interest between the sexes, and conspicuous pre- and postcopulatory struggles. Some species exhibit a mating system that involves much less apparent conflict (type II) and lack the intense copulatory struggles.

I argue that the predominant mating system in water striders is a direct consequence of sexual conflicts over mating decisions. Matings involve high costs to females (increased predation risk and energetic expenditure) but few, if any, balancing direct benefits. Sperm-displacement rates are high, and males thus gain from rematings. Mating frequencies are high; females mate multiply for reasons of convenience. In these species, males are considered to have 'won' the evolutionary conflict over the mating decision in the sense that they have made acceptance of superfluous matings 'the best of a bad job' for females, by evolving behavioral and morphological traits that make it costly for females to reject males attempting copulations. Females, however, have apparently evolved a variety of counter-adaptations to male harassment, to gain control over mating. Further, I suggest that sexual conflict may have played a crucial role in the evolution of type II matings from type I matings.

Water strider mating systems are very plastic. Females assess the rate of male harassment, and make adaptive mating decisions based on this assessment. As a consequence of variation in female mating behavior, the characteristics of the mating system vary with a number of environmental factors. Knowledge of the behavioral dynamics of water strider mating systems makes mechanistic hypotheses of sexual selection possible and provides a framework in which variations between populations in non-random mating and sexual selection can be understood and even accurately predicted. Recent insights gained from the study of water strider mating systems highlight two fruitful research avenues: (1) intraspecific variability of mating systems deserves more attention; and (2) observational and experimental studies at the population level concerned with mating patterns should be linked with experimental studies of behavioral processes at the individual level.

INTRODUCTION

In the past two decades, there has been a marked shift in the way that evolutionary ecologists view sexual behaviors. In the past, ethologists viewed courtship behaviors and mating primarily as harmonious, joint ventures in which males and females cooperated in offspring production. However, it is now widely recognized that male and female evolutionary interests in reproduction may be asymmetrical, and that sexual behavior in many cases represents the resolution of such underlying sexual conflicts (Trivers 1972, 1974; Parker 1979, 1984; Hammerstein and Parker 1987; Alexander *et al.*, this volume). A variety of different conflicts may occur, such as conflicts over isogamous or anisogamous reproduction (Parker *et al.* 1972), relative parental investment (Trivers 1972, 1974), monogamous or polygamous mating systems (Alatalo *et al.* 1981), mating frequency and duration (Parker 1979; Hammerstein and Parker 1987; Arnqvist 1989a; Thornhill and Sauer 1991) and fertilization events (Alexander *et al.*, this volume). This conceptual shift is obvious in the study of water strider sexual behaviors. Mating behavior in this group of bugs typically involves apparent conflicts and dramatic struggles; and several recent papers stress the role of sexual conflicts and female interests in matings (Arnqvist 1988, 1989a, 1992a; Rowe 1992, 1994; Sih and Krupa 1992; Fairbairn 1993; Krupa and Sih 1993; Rowe *et al.* 1994, 1996; Weigensberg and Fairbairn 1994, 1995; Jablonski and Vepsäläinen 1995; Vepsäläinen and Savolainen 1995).

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Water striders (Heteroptera: Gerridae; about 500 species) form an ecologically rather homogenous group of bugs (Andersen 1982; Spence and Andersen 1994). They inhabit water surfaces of a wide range of aquatic habitats and are predators and scavengers, feeding mainly on arthropods trapped at the water surface. Mating and egg-laying continue throughout the reproductive part of the adult life, which lasts from one to three months. The daily fecundity of females ranges from 3 to 15 eggs per female per day for most species. Eggs are typically deposited on floating objects or emergent aquatic vegetation. Water striders are well suited for behavioral studies because of their open and strictly two-dimensional habitat. They can be captured, marked, manipulated and observed easily in their natural environment. They also are kept and reared easily in the laboratory, which makes them an excellent group for experimental studies. Matings are frequent and conspicuous, and there is considerable interspecific variation in mating behavior and sexual dimorphism. As a consequence, there has been a rapidly increasing interest in water strider mating systems, and a growing literature has proven water striders to be suitable for addressing many general issues about the evolution of mating systems.

The main goals of this paper are to (1) provide a comparative review of water strider mating behaviors; (2) discuss the role of sexual conflicts in the evolution of water strider mating systems; and (3) identify causal links between sexual behavior and sexual dimorphism in secondary sexual traits. Although my basic intent is to review current knowledge, I also hope that my development of the subject will prove to be provocative and hence stimulate new creative research in the field.

MATING BEHAVIOR

The literature on water strider mating behavior is rather comprehensive; I have been able to gather information on the sexual behavior of 30 species (Table 8-1). However, the information available for different species varies from single casual observational notes to thorough experimental studies. Information on temperate species is relatively satisfactory; descriptions of mating behavior of most tropical and subtropical species typically are absent or more incomplete. Even though there is considerable inter- and intraspecific variation in sexual behavior, I suggest that there is a basic dichotomy in the mating behavior of water striders and that matings can be divided into two distinct types.

Type I mating behavior

Most species of water striders studied to date exhibit type I matings, where five mating phases can be distinguished (Fig. 8-1) (Arnqvist 1988; Rowe 1992). Males may use two tactics to find potential mates; in most cases they search actively for females, but males of some species may also be territorial and use a sit-and-wait strategy (Hayashi 1985; Nummelin 1988). When females are encountered, males typically initiate matings by simply lunging at females, without persuasive courtship (cf. Alexander *et al.*, this volume). Although males of some species use ripple signals to determine the sex of other individuals (see Wilcox 1979; Wilcox and Stefano 1991), males are generally indiscriminate in their efforts; males of many species lunge at both conspecific and heterospecific males. A male that successfully contacts a female will grasp her thorax with his forelegs and rapidly attempt to insert his genitalia. Females almost invariably respond with some form of resistance, and they may use several different behaviors in their attempts to dislodge the male. One common reluctance behavior has been termed 'somersaulting' (Fig. 8-2) (Arnqvist 1989b; Rowe 1992), in which the female rears her midlegs, which causes the pair to flip over backwards or sideways, often while she uses her forelegs to try to break the male's grasp with his forelegs. These backward somersaults are performed repeatedly, often combined with other behaviors such as jumps and/or jerks. During this precopulatory struggle females are trying to forcefully dislodge males while males are trying to endure this resistance (Andersen 1982; Arnqvist 1989b, 1992a; Krupa *et al.* 1990; Rowe 1992; Spence and Andersen 1994). The duration of the precopulatory struggle ranges from a few seconds to several minutes (Arnqvist 1992a; Rowe 1992; Weigensberg and Fairbairn 1994; Arnqvist and Rowe 1995). In many species, females are usually successful in dislodging males; in *Gerris odontogaster* and *G. buenoi* females have been reported to dislodge the male in approximately 80% of the struggles (Arnqvist 1989b; Rowe 1992) and more than half of the precopulatory struggles end with male dislodgment in *Aquarius remigis* (Weigensberg and Fairbairn 1994). However, in *G. lateralis* and *G. lacustris* males seem better able to overcome female reluctance; males of these species have been reported to 'win' more than half of the precopulatory struggles (Arnqvist 1988; Vepsäläinen and Savolainen 1995). Female *A. najas* appear almost incapable of dislodging males, despite vigorous struggling (Sattler 1957).

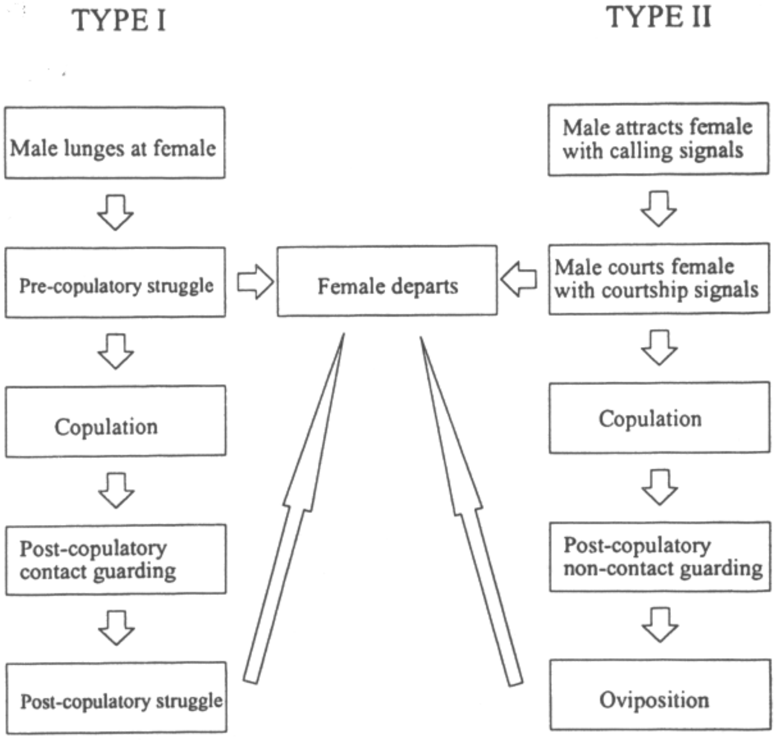

Fig. 8-1. A generalized flow chart of the mating sequence of type I and type II matings in water striders. See text for further details.

Copulation starts if female reluctance desists and the male inserts his genitalia successfully. Average copulation duration ranges from 5 to 20 minutes in most species (Table 8-1), one notable exception being *A. remigis* where the pair may remain *in copula* with joined genitalia for up to many hours (see, for example, Clark 1988; Fairbairn 1988).

Most species of water striders exhibit postcopulatory contact guarding. After retracting his genitalia, the male remains mounted on top of the female without genital contact. The duration of guarding is highly variable both within and between species, and may last from some minutes to several hours (Table 8-1). The longest postcopulatory guarding reported occurs in *A. najas*, where the pair may remain in contact for several days or even several weeks (Sattler 1957; Murray and Giller 1990)!

Type I matings are normally terminated with a postcopulatory struggle. During this phase, the female once again struggles to dislodge the male while the male attempts to remain coupled. Again, there is considerable variation between different species in the ability of the male to endure the postcopulatory struggle. Males of *G. buenoi* and *A. remigis* are almost invariably dislodged during the

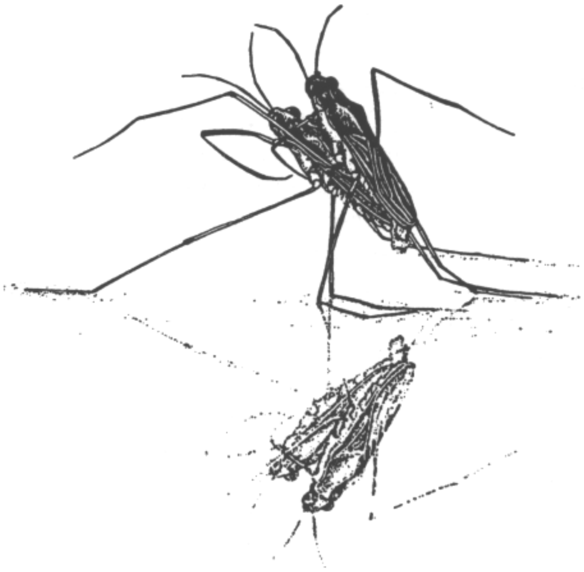

Fig. 8-2. A pair of *Gerris odontogaster* engaged in a precopulatory struggle. The male has successfully grasped the female and attempts copulation, but the female resists by rearing her midlegs, causing the pair to repeatedly 'somersault' backwards or sideways (reprinted with permission from Rowe *et al.* 1994).

first struggle (Rowe 1992; Weigensberg and Fairbairn 1994), whereas males of *G. lateralis* and *G. lacustris* often can endure several consecutive struggles (Arnqvist 1988; Jablonski and Vepsäläinen 1995). There is also considerable variation within species in how matings are terminated; males of some species may terminate matings without preceding struggle under some environmental circumstances (Erlandsson 1992; Weigensberg and Fairbairn 1994; Vepsäläinen and Savolainen 1995).

Type II mating behavior

Type II matings differ from type I matings mainly in that males 'court' females with ripple signals, there is much less apparent conflict, and fewer aggressive elements are involved (Fig. 8-1). Males are typically territorial, defending suitable oviposition sites situated in the territory. Males of several species anchor themselves to the oviposition site with the legs and produce calling signals, which apparently attract receptive females (Wilcox 1972; Hayashi 1985; Nummelin 1988). Males respond aggressively to other males, and emit repel signals and engage in fights to defend their territory. In contrast, when a female approaches, the male will switch from calling signals to different types of courtship signals. During courtship, the female often inspects the oviposition site carefully and may either (1) reject the object and skate away or (2) accept the site and allow the male to mount her without much reluctance. The male then inserts his genitalia and a comparatively brief copulation follows (copulation duration normally one or a few minutes; see Table 8-1).

In contrast to type I matings, type II matings typically involve postcopulatory non-contact guarding (Fig. 8-1). After copulation, the male dismounts and backs off from the female a few centimeters. The female will then oviposit, and the male stays in immediate proximity to the female during oviposition and guards her from disturbance of other males. Males approaching the ovipositing female will be aggressively warded off by the guarding male during the 10–20 min that oviposition may take. After ovipositing, females leave the site, and males return to producing calling signals. Hence, in type II matings there is usually a direct association between copulation and female oviposition, which is not normally the case in type I matings.

Pure type II matings as described above have been reported from species in the genus *Rhagadotarsus* (Wilcox 1972; Nummelin 1988) and in *A. elongatus* (Hayashi 1985). In the holarctic genus *Limnoporus*, type II matings differ somewhat from the description above, and even share some characteristics of type I matings (Spence and Wilcox 1986; Wilcox and Spence 1986; Nummelin 1987; J. R. Spence, unpublished). First, territorial males do not seem to attract females actively by producing calling signals, but rather sit and wait for receptive females. Second, males generally stay mounted on top of females during oviposition, i.e. they exhibit a mate-guarding behavior much as in type I matings. Third, females sometimes show reluctance to mate even when courted by a signaling male, and females generally terminate matings.

Mating systems

Mating activity is very high in most species of water strider. Both sexes copulate repeatedly in all species studied, although the mating frequency varies with species and environmental conditions. Wilcox (1972) reports a maximum male mating frequency of five matings in one hour in *R. anomalus*. Typically, however, females as well as males have been reported to mate from 'a few' up to 'several' times per day throughout their reproductive lives, both in the field and in the laboratory (see, for example, Vepsäläinen 1974; Arnqvist 1989b, 1992b; Rowe 1992; Sih *et al.* 1990).

Female water striders are polyandrous, although there is extensive variation in female mating frequency between species. Following the classification of mating systems by Thornhill and Alcock (1983), female water strider mating systems are best described as convenience polyandry (Arnqvist 1989a; Rowe 1992; Weigensberg and Fairbairn 1994). This is true at least for mating systems characterized by type I matings. Water strider males of all species are polygynous, and there are two basic male mating systems. Mating systems where type I matings predominate are best characterized as scramble competition polygyny, since males do not monopolize either females, resources or specific sites. In cases where type II matings are involved, males provide females with oviposition sites and defense from harassment by other males, and these systems are thus best described as resource defense polygyny. *Limnoporus* species and *A. elongatus* exhibit a mixture of these two male mating systems.

In many species, the optimal behavior for acquiring matings varies with environmental conditions (e.g. sex ratio and density) and individual state (e.g. size and nutritional state), and thus males may adopt several different mating tactics

Table 8-1. *Taxonomic distribution of mating behaviors in water striders*

Subfamily	Species	Female body size (mm)	Body size dimorphism ratio (F/M)	Precopulatory struggle	Mating behavior	Copulation duration	Postcopulatory contact guarding duration	Termination of mating	References
Rhagadotarsinae	*Rhagadotarsus anomalus*	4.6	1.18	No	Type II	1 min	None[e]	Male	1
	Rhagadotarsus hutchinsoni	—	—	No	Type II	0.8 min	None[e]	Male	2
Gerrinae	*Aquarius conformis*	16.4	1.09	Yes (less frequent)	Type I	<5 min	123 min (30–790)	—	4, 35
	Aquarius elongatus	24.4	1.03	Only occasionally	Type I & II	4–5 min	None[e]	—	28
	Aquarius najas	16.5	1.28	Yes	Type I	1–4 min	hours–weeks (!)	—	9, 25, 26, 27
	Aquarius paludum	15.4	1.12	Yes	Type I	10 min[b]		Female[a,c]	9
	Aquarius remigis	13.1	1.08	Yes	Type I	20–>400 min[a]	None[f]	Female[a,c]	4, 5, 21, 22, 23, 24
	Gerris argentatus	7.4	1.13	Yes	Type I	10–20 min[a,b]		Female[a,c]	9
	Gerris buenoi	8.1	1.11	Yes	Type I	7.1–17.8 min[a]	16.4–83.0 min[a]	Female	3, 4, 5
	Gerris comatus	10.5	1.13	Yes	Type I	18.9 min[b]		Female	4, 5, 13
	Gerris gillettei	9.1	1.07	Yes	Type I	14.2 min	19.1 min	Female	37
	Gerris incognitus	9.1	1.08	Yes	Type I	10.9 min	30 min (0–110)	Female	39
	Gerris insperatus	10.4	1.10	Yes	Type I	31.6 min[b]		—	4, 20
	Gerris lacustris	9.7	1.11	Yes	Type I	5–20 min[a]	5–40 min[a]	Female[a,c]	9, 10, 11, 36
	Gerris lateralis	10.1	1.12	Yes	Type I	16.2 min	60–>120 min[a]	Female	8, 9
	Gerris marginatus	9.8	1.09	—	Type I	10.3 min[b]		—	4
	Gerris odontogaster	8.7	1.10	Yes	Type I	10–15 min[a]	40–90 min[a]	Female	6, 7
	Gerris pingreensis	8.9	1.02	Yes	Type I	—	—	—	13, 20
	Gerris swakopensis	—	1.07[d]	Yes	Type I	8.2 min	—	Female	2
	Gerris thoracicus	11.9	1.11	Yes	Type I	—	—	—	12
	Limnoporus dissortis	14.0	1.06	Yes	Type I & II	5–25 min	5–20 min	Female	4, 17, 18, 19, 20, 36
	Limnoporus notabilis	18.1	1.04	Yes	Type I & II	5–20 min	5–20 min	Female	4, 17, 18, 19, 20, 36
	Limnporus rufoscutellatus	15.5	1.09	Yes	Type I & II	10 min	>1 hour	Female	9, 14, 15, 16, 17, 36
	Tenagogonus albovittatus	—	1.06[d]	Yes	Type I	—	—	—	2
Cylindrostethinae	*Potamobates tridentatus*	—	—	Yes	Type I	many hours[b]		—	29
Halobatinae	*Eurymetra natalensis*	—	0.98[d]	Yes	Type I	10 min	—	—	2
	Halobates fijiensis	—	<1.00	—	—	0.25–2 min[b]		—	31
	Halobates robustus	5.0	1.25	—	—	many hours[b]		—	30
	Metrocoris histrio	5.8	1.02	Yes	Type I	several min[b]		Female	33, 34
	Metrocoris tenuicornis	3.9	0.81	Yes	Type I	5–10 min[b]		—	32

[a] Found to be variable, depending on environmental conditions; [b] only mating duration reported (i.e. copulation plus guarding); [c] male reported to terminate mating occasionally; [d] size ratio based on leg lengths; [e] non-contact guarding occurs; [f] species exhibits prolonged copulation.

Source: 1 Wilcox (1972); 2 Nummelin (1988); 3 Rowe (1992); 4 Fairbairn (1990); 5 Fairbairn (1988); 6 Arnqvist (1992a); 7 Arnqvist (1992b); 8 Arnqvist (1988); 9 Erlandsson (1992); 10 Vepsäläinen and Savolainen (1995); 11 Jablonski and Vepsäläinen (1995); 12 Kaitala (1991); 13 Spence (1979); 14 Vepsäläinen and Nummelin (1985b); 15 Vepsäläinen (1985); 16 Nummelin (1987); 17 Andersen and Spence (1992); 18 Wilcox and Spence (1986); 19 Spence and Wilcox (1986); 20 J. R. Spence (unpublished); 21 Wilcox (1979); 22 Sih *et al.* (1990); 23 Rubenstein (1989); 24 Clark (1988); 25 Sattler (1957); 26 Vepsäläinen and Nummelin (1985a); 27 Murray and Giller (1990); 28 Hayashi (1985); 29 Wheelwright and Wilkinson (1985); 30 Foster and Treherne (1982); 31 Foster and Treherne (1986); 32 Cheng (1966); 33 Ban *et al.* (1988); 34 Koga and Hayashi (1993); 35 J. J. Krupa (unpubl.); 36 Andersen (1994); 37 G. Arnqvist (unpublished).

(Dominey 1984). This is true for water striders as well (Spence and Andersen 1994), where two main categories of alternative male mating behavior may be distinguished.

1. In some species with type I matings, males have been shown to utilize two different mate-searching tactics. Most individuals normally cruise around and search for females actively, but some males are more site-specific. These males will expel approaching males aggressively and attempt to mate with approaching females. This category of alternative mate-searching behaviors is found in *G. swakopensis*, where territorial males attack all other approaching water striders (Nummelin 1988). Attacks on intruding males and females look essentially identical, but other males are repelled whereas attacks on females result in mating attempts. Switches between similar alternative male mate-searching tactics occur in *Tenagogonus albovittatus*, *Eurymetra natalensis* and *Metrocoris histrio* (Nummelin 1988; Koga and Hayashi 1993).
2. A more complex behavioral flexibility occurs in males of some of the species that exhibit type II matings. Males adopting a type II mating behavior may not always be territorial but may actively search for females to court. If a female is encountered, the male will emit courtship signals in the same manner as a territorial male (Vepsäläinen and Nummelin 1985a,b; Spence and Wilcox 1986). These two tactics represent different means of finding potential mates, and are in that respect analogous to the behavioral dimorphism mentioned above for type I matings. However, a more profound polymorphism also occurs. Males sometimes do not signal to females with ripple signals but instead lunge at and grasp females and attempt to insert the genitalia (Hayashi 1985; Spence and Wilcox 1986; Wilcox and Spence 1986). Females will typically try to dislodge these males by intensive struggling, and males will attempt to subdue reluctant females much in the same way as in type I matings (Spence unpublished). Males adopting this tactic may either actively search for females or sit and wait (Hayashi 1985; Spence and Wilcox 1986). To summarize, males exhibiting type II matings may also attempt to grasp females without prior courtship in a way closely resembling type I matings. Irrespective of which of these two tactics a male uses to achieve a mating once a female is encountered, he may either search actively for females or use a more sedentary tactic in order to find potential mates.

Both individual state and environmental conditions have been shown to affect male choice of mating tactic. In some species, large males have been shown to more frequently be territorial (Hayashi 1985; Nummelin 1988), but age may also affect the choice of behavior (Koga and Hayashi 1993). In contrast, nutritional state does not seem to affect male choice of mating behavior (Spence and Wilcox 1986; Rowe *et al.* 1996). The presence and distribution of females in the habitat affect male mating tactics, as does the availability of suitable oviposition sites (Nummelin 1988; Hayashi 1985). However, there is a wide range of factors, both state variables (e.g. parasite load, previous mating history) and environmental factors (e.g. predator presence, population density, sex ratio, microhabitat structure) as well as interactions among these, that may influence the choice of male mating tactic but have not yet been addressed in experimental studies.

SEXUAL CONFLICTS OVER MATING

There is a basic sexual asymmetry in the relative interests in matings for animals in general. The reproductive success of males is intimately associated with the number of females they mate, whereas for females a single mating is often enough to achieve more or less maximum success. In other words, it often pays males but not females to search for additional matings, and in encounters between males and females of many species, males are under selection to mate whereas females are under selection not to mate (Parker 1979; Alexander *et al.*, this volume). This type of basic sexual conflict is thus a conflict over the mating decision. In addition to this conflict, there may also be conflicts over the mating duration (Parker 1979; Thornhill and Sauer 1991). If a female mates multiply, there may be sperm competition between males over the fertilization of the female's ova. In many arthropods, males benefit by prolonging matings to reduce the degree of sperm competition (Parker 1970; Alcock 1994). However, females may not benefit by this behavior, and in cases where the 'optimal' mating duration differs between the sexes a conflict over the mating duration will occur.

Parker (1979) stressed that it is often extremely difficult to study sexual conflicts, because of the difficulty of measuring the costs and benefits involved in matings. In water striders, there is strong apparent conflict over both the mating decision (precopulatory struggles) and the mating duration (postcopulatory struggles). Furthermore, a number of studies have addressed the relative costs and benefits involved in matings. Water striders thus provide an excellent group for evaluating costs and benefits involved in matings and for studying the dynamics of sexual conflicts.

The costs and benefits of mating for males

There may be a number of costs of mating for males, the most universal being the time and energy devoted to mating and the energetic costs of gamete production (Daly 1978; Dewsbury 1982). Although there are no direct data on the cost of ejaculate production in male water striders, two lines of evidence suggests that it is relatively low. First, water strider ejaculates consist of little more than sperm, i.e. there are no nutritious accessory substances (Andersen 1982; see below). Second, maximum male mating frequency is often high and refractory periods typically short.

In species where females mate with more than one male, one of the major factors that affects the evolution of mating systems is the sperm utilization pattern of females (Walker 1980; Smith 1984). Three different studies have addressed the degree of sperm displacement in water striders. Using reversed double mating experiments with sterilized males, Arnqvist (1988) showed that approximately 80% of a female's eggs were fertilized by the last male to mate in *G. lateralis*. Rubenstein (1989) demonstrated with a similar technique that last male advantage was in average 65% in *A. remigis*, and that the degree of sperm displacement was partly related to copulation duration. Finally, use of a genetic marker has shown sperm displacement rates of more than 90% in *Limnoporus dissortis* and *L. notabilis* (J. R. Spence, unpublished). Thus, when water strider females remate, the last male to mate will fertilize the majority of the female's eggs, even if the rate of sperm displacement may vary among species.

Because last-male sperm precedence occurs in water striders, there is strong selection in males to reduce sperm competition by other males. By guarding a female after sperm transfer, a male reduces the risk of the female mating with another male before she oviposits, but decreases his probability of finding additional mates (Parker 1974; Alcock 1994; Jablonski and Kaczanowski 1995). Although there is little field data (but see Rowe 1992), it appears as if water strider males often attempt to guard females until oviposition occurs, but that males are mostly dislodged prior to oviposition (Rowe 1992; Jablonski and Kaczanowski 1995; Jablonski and Vepsäläinen 1995). Three different mate-guarding tactics have evolved within the family.

1. In most water striders, the male will withdraw his genitalia after the relatively brief copulation but remain mounted on top of the female. The female will carry the passive non-copulating male during this postcopulatory contact guarding phase, typical for type I matings. There is considerable variation in guarding duration (both inter- and intraspecifically). The position of the male relative to the female during guarding also varies between species. In *Limnogonus* and some *Halobates* species, the male is positioned far back on the female and may even be towed rather than carried by the female (Andersen 1982). In *M. tenuicornis*, but not in the congeneric *M. histrio* (Ban *et al.* 1988; Koga and Hayashi 1993), the sex roles are reversed so that the male carries the passive female below (Cheng 1966).
2. In some species, the male dismounts after copulation but remains close to the female. The guarding male will be aggressive towards males, and repel intruders. This type of postcopulatory non-contact guarding has been described in species with typical type II matings, i.e. in the *Rhagadotarsus* species (Wilcox 1972; Nummelin 1988) and in *A. elongatus* (Hayashi 1985).
3. If males prolong copulations beyond the time necessary for insemination, males may actually be guarding females by acting as living mating plugs (Sillén-Tullberg 1981; Thornhill and Alcock 1983). This strategy has so far only been described for one species of water strider, *A. remigis*. In this species, complete sperm transfer takes approximately 20 min (Rubenstein 1989), but males typically prolong copulations and may remain *in copula* with inserted genitalia for as long as many hours (Wilcox 1984; Clark 1988; Rubenstein 1989; Sih *et al.* 1990; Fairbairn 1990).

The costs and benefits of mating for females

Females may bear a number of potential costs in matings, such as time and energy costs, increased predation risk and risk of injury or disease transmission. However, several benefits (e.g. replenishment of sperm, reception of nutrients from mating males or various genetic benefits) may balance these costs (Thornhill and Alcock 1983; Arnqvist 1989a; Dickinson, this volume).

In many insect species, females are thought to mate multiply in order to replenish their depleted sperm supplies (Thornhill and Alcock 1983). However, this is clearly not the case in water striders. Females have been found to be able to store viable sperm for extensive periods of time without reduction in fertility in several species. Sperm longevities have been reported to be over 14 d in *G. thoracicus*, over 30 d in *G. lateralis*, over 10 d in *G. odontogaster* and over 24 d in *A. remigis* (Kaitala 1987; Arnqvist 1988, 1989a; Rubenstein 1989). Neither do female water striders gain any major nutritional benefits via the ejaculate (Andersen 1982; Kaitala 1987; Arnqvist 1989a; cf. Gwynne, this volume), nor any major genetic benefits (Arnqvist 1989a), from rematings.

It is often assumed that mating activities increase the risk of predation. Water striders are particularly well studied from this point of view; three independent studies have shown that the risk of predation increases during mating. Arnqvist (1989a) showed that the risk of predation from backswimmers increased by a factor of three for female *G. odontogaster* as a consequence of mating activities. Fairbairn (1993) recorded a doubled risk of predation from frogs for mating compared with single *A. remigis* females, and Rowe (1994) demonstrated that mating *G. buenoi* females suffered two to three times greater predation risk from backswimmers than did single females. The increase in predation risk for females during mating is a combined effect of increased visibility and a decreased escape ability when attacked (Fairbairn 1993; Rowe 1994). The pre- and postcopulatory struggles are especially risky parts of mating: Rowe (1994) reported that struggles attract predators, and that predators were about five times as successful in attacks on struggling pairs compared with single individuals. Furthermore, in attacks on mating pairs, females are taken as prey more often than males (Arnqvist 1989a; Rowe 1994).

Male harassment, copulation and guarding may also be energetically costly for females (Stone 1995). Females of both *G. odontogaster* and *A. remigis* suffer from reduced mobility during mating (Arnqvist 1989a; Fairbairn 1993). Because water striders typically skate around searching for food, this will probably result in either a reduced foraging success for equal effort or a higher energetic effort for equal foraging success compared with single females (Arnqvist 1989a; Fairbairn 1993; but see below).

Form and resolution of sexual conflict

The primary interests in matings of water strider males and females are thus asymmetric, and two types of sexual conflicts occur. Males benefit from rematings in terms of paternity at little cost; females do not receive any measurable benefits from rematings but suffer energetic costs and increased predation risk. In encounters between males and females, a conflict over the control of the mating decision thus typically occurs. Similarly, males benefit from mate-guarding phases in terms of decreased sperm competition, whereas contact guardings are costly for females. Thus a conflict over the control of the mating duration also often occurs.

Thornhill and Alcock (1983) suggested that if males can evolve behavioral and/or morphological traits that make it costly for females to reject males attempting copulation, females may mate for reasons of convenience. This is exactly what has been suggested to occur in water striders with type I matings (Rubenstein 1984; Wilcox 1984; Arnqvist 1989a, 1992a; Rowe 1992; Vepsäläinen and Savolainen 1995). Arnqvist (1992a) modeled this situation and showed that water strider females making 'the best of a bad job' should resist matings, but only to a certain point representing a trade-off between the costs of rejecting harassing males and the costs of mating. Rowe (1992) arrived at similar conclusions in a verbal treatment of the situation for *G. buenoi*. This model of water strider mating dynamics has been shown to accurately predict adaptive female mating behavior in several species (Arnqvist 1992a; Rowe 1992; Sih and Krupa 1992; Krupa and Sih 1993; Vepsäläinen and Savolainen 1995; Weigensberg and Fairbairn 1994); when the rate of male harassment is high, single females have little to gain from resisting matings since they will be repeatedly harassed if the male is dislodged, and consequently females do not struggle as intensively during the precopulatory struggle before accepting a copulation. As a result, mating frequencies and mating durations increase. In contrast, when harassment rates are low, a female that dislodges a male will enjoy a relatively long period before the next harassment, and females struggle more intensively to dislodge males attempting copulations.

In water strider species with type I matings, females carrying males are not harassed as frequently or intensively as are single females; males will occasionally lunge at mating pairs but make no serious mating attempts. Wilcox (1984) showed that *A. remigis* females could even forage more effectively when carrying a male compared than when single, as a consequence of reduced harassment rates on mating pairs; he suggested that females in this way may actually 'benefit' from matings (see also Rowe *et al.* 1996). Thus, even though there is a basic sexual conflict over mating (females would be better off foraging singly given that they could effectively avoid males or reject matings at a very low cost), male water striders have in effect inflicted an apparent harmony between the sexes on females by frequent and effective harassment. Males thus seem to have made acceptance of superfluous matings 'the best of a bad job' for females in many situations (Arnqvist 1992a).

In addition to the conflict over the mating decision, there is likely to be a related conflict over the mating duration. These two conflicts are reflected in the two conspicuous fights typical for type I matings: the pre- and postcopulatory struggles. Although the various female costs of long vs. short matings have not been formally modeled, some obvious predictions can be made (Wilcox 1984; Arnqvist 1992a; Rowe 1992; Vepsäläinen and Savolainen 1995). The most intuitive prediction is that females should accept longer matings (before dislodging the male) when harassment rates are high. This prediction has been confirmed in a number of experimental studies, where mating duration has been found to increase with increased sex ratio and/or density (Clark 1988; Arnqvist 1992a; Rowe 1992; Erlandsson 1992; Jablonski and Vepsäläinen 1995; Vepsäläinen and Savolainen 1995).

Although the options for a female during the pre- and postcopulatory struggles are essentially the same, i.e. dislodging the male means avoiding the costs of carrying the male around and accepting the male means that these costs will be experienced for a certain time, the consequences of 'winning or losing' are different for males. In the precopulatory struggle, males struggle to achieve a copulation or not. In the postcopulatory struggle, males struggle to reduce sperm competition (i.e. to increase the quality of the already achieved copulation). Thus, males should always choose higher persistent time and effort than females during the precopulatory struggle (i.e. males should never withdraw, but may nevertheless be dislodged), and female interests alone should determine the outcome of precopulatory struggles (Arnqvist 1992a). This expectation seems to be consistent with the struggling behavior in type I matings (Rowe 1992). The conflict over the mating duration is theoretically more complex than the conflict over the mating decision, because both male and female interests have to be considered (Vepsäläinen and Savolainen 1995). For example, it is possible to envision situations (i.e. strongly female-biassed sex ratios) where males should not guard females from sperm competition, but rather invest time in searching for additional mates (Parker 1974; Alcock 1994). However, because harassment rates also decrease in such situations, female interests act in the same direction; females should accept only short matings. In such situations, the conflict over the mating duration may diminish and males are predicted to terminate matings shortly after copulation without struggle. Such a behavioral pattern has been observed (Erlandsson 1992; Vepsäläinen and Savolainen 1995). Thus, when harassment rates are low both sexes should favor short matings and vice versa, and it is not obvious when and why the optimal mating duration should differ between the sexes. This issue clearly needs a formal theoretical treatment, especially as a number of factors other than sex ratio should affect the pros and cons of various mating durations for females and males (Sih *et al.* 1990; Arnqvist 1992a; Rowe *et al.* 1994).

It is tempting to view the sexual conflict over mating decisions in water striders as evolutionary 'wars of attrition' (Hammerstein and Parker 1987; Clutton-Brock and Parker 1995; Alexander *et al.*, this volume). Even though females in one sense may 'control' matings by their reluctance (Rowe 1992), males may be said to have won the 'battle of the sexes' in the sense that they have apparently succeeded in making it costly for females to resist matings. I suggest that two major factors have made the evolution of this mating system possible. First, male behavioral and morphological traits make it costly for females to resist matings. Water striders are well adapted to determine the direction and distance of objects at the water surface (Jamiesson and Scudder 1979; Andersen 1982), and males often succeed in lunging at females from distances of up to 10–15 times their own body length (Arnqvist 1989b). Males of many species have also evolved various morphological adaptations that increase their grasping ability (see below), which makes it more costly for females to dislodge them. Second, habitat characteristics make it difficult or even impossible for females to avoid males. The water surface is a strictly two-dimensional habitat with a relatively low degree of complexity. Furthermore, females have to be active in highly predictable areas in order to forage and oviposit. Thus, in contrast to many other insects (see, for example, Wiklund 1982; Wickman 1986), avoiding males is often difficult for female water striders (Krupa *et al.* 1990) and males are typically found searching for females in areas where females forage (Wilcox 1984; Krupa *et al.* 1990) or oviposit (Hayashi 1985; Foster and Treherne 1986). Under this scenario, the resolution of the sexual conflict will be dynamic and depend on behavioral, morphological and constitutional adaptations within each sex as well as on the environment. The relative ability of the sexes to control matings should then differ within and between species, which is exactly what we observe.

EVOLUTION OF WATER STRIDER MATING SYSTEMS

The least specialized and most common water strider mating system, female convenience polyandry associated with type I mating behavior, is most likely the plesiomorphic mating system within the Gerridae, as shown primarily by comparisons with outgroups (Andersen 1982). A simple mating system where the male jumps on the back of the female without prior courtship, grasps her and attempts copulation while the female attempts to dislodge the male has been described for several other families in the infraorder Gerromorpha (i.e. Veliidae (Andersen 1982, 1989) and Hebridae (Heming-van Battum and Heming 1989)).

Type II matings appear to have evolved independently at least three times within the Gerridae: in the genus *Rhagadotarsus* in the subfamily Rhagadotarsinae and in the *Limnoporus rufoscutellatus* group and the *Aquarius conformis* group within the subfamily Gerrinae (Andersen 1982, 1990, 1994; Wilcox and Spence 1986; Andersen and Spence 1992). This trend indicates that fairly general selective mechanisms are responsible for the evolution of type II from type I matings.

Finding environmental or constitutional correlates of interspecific variation in a trait is crucial in evaluating adaptive hypotheses about the evolution of the trait (Harvey and Pagel 1991; Rutowski, this volume). For the evolution of type II mating behavior from type I in water striders, it is difficult to find any such correlates. Species with type II matings occur in various kinds of habitats, e.g. in both lotic and lentic as well as in both temporary and permanent habitats, and there is no reason to believe that resources (e.g. oviposition sites) are more limited, predictable or clumped in type II species (Spence and Wilcox 1986; G. Arnqvist, personal observations). Spence and Wilcox (1986) suggested that egg parasitoids may play a role, but these are also known to infest eggs of many species with type I matings and more recent studies indicate that territoriality may actually increase parasitism (Henriquez and Spence 1993). Further, species with type I and type II matings do not differ markedly in general morphology, size or in sexual size dimorphism (Table 8-1).

I suggest that sexual conflict has played a crucial role in the evolution of type II systems from type I systems in water striders. If females can evolve attributes that in any way increase their control of mating initiation by reducing the effectiveness of male harassment, it may be more profitable for males to be sedentary, less aggressive, and harass females primarily at oviposition sites. As in other insects (Martens and Rehfeldt 1989), female water striders are particularly sensitive to male harassment during oviposition, because escaping harassment means interrupting oviposition. *Limnoporus* females have actually been found to lay more eggs if protected from harassment and interference during oviposition by a guarding male (Spence and Wilcox 1986). Thus, although females may be said to trade matings against temporary protection from further harassment during foraging and normal activity in type I matings, type II systems may have evolved by females trading matings against protection from harassment during oviposition. There are a number of potential factors that may promote such an evolutionary pathway, of which at least two have some empirical support. (1) Females may evolve morphological attributes that decrease the cost of rejecting unwanted mates, and thus shift the resolution of the mating conflict towards female interests. This seem to have occurred in *G. incognitus* (Arnqvist and Rowe 1995), and, interestingly enough, the mating system is affected: males of this species seem to be less aggressive and harass females primarily at oviposition sites. (2) A high degree of sperm displacement generally selects for an equally high degree of temporal proximity between mating and oviposition (Parker 1974; Walker 1980). If sperm precedence is very high, waiting for and/or harassing females at the oviposition sites may be a better option for males than searching and mating more randomly in space and time. Available data on sperm-displacement rates is very limited, but is at least in accordance with this hypothesis: the estimate of sperm precedence is higher in *Limnoporus* (>90%) than in species with type I matings (50–80%). The evolution of type II matings from type I matings in water striders may thus be an example of Walker's (1980) suggestion that females determine optimal male mating behavior, by the structure and/or function of their reproductive tract. However, more comparative data on sperm-displacement rates in water striders is needed to evaluate this latter hypothesis.

When discussing phylogenetic patterns of mating systems, one important aspect is to assess the degree of phylogenetic constraints (*sensu* Arnold 1992) on mating behavior. In water striders, some observations indicate a very low degree of phylogenetic constraints on behavior. One is the enormous diversity of mating behaviors found within the single genus *Aquarius*. In this genus, some species (*A. remigis*, *A. najas*, *A. conformis* and *A. paludum*) exhibit type I matings, whereas typical type II matings occur in *A. elongatus*. Further, mating durations range from very short (*A. elongatus*) to the longest ever observed within the Gerridae (*A. najas*). Males of some species show alternative mating tactics, whereas others do not; all three of the male mate-guarding tactics that have evolved in Gerridae are found within this single genus. The intensity of precopulatory conflicts also varies markedly between *Aquarius* species with type I matings (J. J. Krupa, unpublished). High variation in mating behavior has also been observed in the ocean skaters *Halobates* (Foster and Treherne 1982, 1986), in *Metrocoris* (cf. Cheng 1966; Ban *et al.* 1988; Koga and Hayashi 1993), in *Gerris* (Nummelin 1988) and in *Limnoporus* (Klingenberg and Spence 1994; J. R. Spence, unpublished). Put together, these high levels of intrageneric variability in behavior suggest that phylogenetic constraints on sexual behavior are not very strong within Gerridae, and that other factors shape mating systems adaptively (Spence and Andersen 1994; Andersen 1994).

SEXUAL DIMORPHISM AND SEXUAL SELECTION

The most consistently dimorphic trait in water striders is size: females are larger than males in most species (Andersen 1982, 1994; Fairbairn 1990; Spence and Andersen 1994; Table 8-1). The average female : male size ratio is about 1.1 within the family (range 0.81–1.32). There is considerable size-ratio variation within subfamilies and even within genera. In some species the size distribution of males is distinctly bimodal, some males being larger and some smaller than females (Andersen 1982; Chen and Nieser 1993). The function of this male dimorphism is unfortunately unknown.

Water strider males also exhibit three other types of sexual dimorphism: (1) modifications of the genital segments, (2) modifications of the legs and (3) modification of body shape. (1) The genital and pregenital abdominal segments are modified in most species of water strider, and are often provided with outgrowths of various shape and form (Andersen 1982, 1991; Arnqvist 1989b). These may be minor modifications, but in many species or genera male genital segments are large and conspicuous. For example, in *Ptilomera* the male suranal plate is enlarged, flat and conspicuous and often provided with remarkable lateral projections (Hungerford and Matsuda 1965). Male *Halobates* typically have very conspicuous genitalia; the eighth abdominal segment is provided with various processes and the proctiger is broad and flattened (Andersen 1991; Andersen and Foster 1992). In *G. odontogaster*, males are provided with ventral processes on the seventh abdominal segment (Arnqvist 1989b). (2) Male water striders also generally have thicker and more powerful forelegs than females, despite their smaller body size (Sattler 1957; Andersen 1982; Rubenstein 1984). In addition, the male forefemora are equipped with pegs, spines, bristles and/or hair tufts in many species (for example in the genera *Amemboa*, *Metrocoris*, *Ptilomera*, *Asclepios* and *Halobates*). However, not only the forelegs may be sexually dimorphic. The most extreme male modifications of appendages occur in *Rheumatobates* (Hungerford 1954), where the antennae are modified to powerful leg-like structures and the hindlegs are curved and provided with the most bizarre outgrowths, pegs, spines and tufts of hair (see Fig. 8-3 and figures in Hungerford 1954). None of these structures occurs in females. (3) In many species there is also sexual dimorphism in body shape. Typically, the ventral surface of the abdomen is flattened, thinned or even depressed in males. This is obvious in the *Aquarius najas* group and in the *G. gillettei* group (Andersen 1990, 1993).

There are relatively few studies where sexual selection has been estimated in natural populations of water striders. Those that have been published have all been cross-sectional studies (but see Preziosi and Fairbairn 1996), where mating and single males have been compared in various ways. Several male traits have been claimed to be subjected to sexual selection in different species. Selection for large male size has been found in *G. buenoi*, *G. lateralis*, *G. lacustris*, *A. remigis* and *A. elongatus* (Hayashi 1985; Fairbairn 1988; Sih and Krupa 1992; Fairbairn and Preziosi 1994; Krupa and Sih 1993; Preziosi and Fairbairn 1996; Rowe and Arnqvist 1996), whereas selection for small male size has been reported in *G. buenoi*, *G. odontogaster* and *A. remigis* (Fairbairn 1988; Arnqvist 1992c; Kaitala and Dingle 1993; Blanckenhorn *et al.* 1995). Sexual selection for wide male forefemora and long genital segments have been demonstrated in *A. remigis* males (Rubenstein 1984; Weigensberg and Fairbairn 1995; Preziosi and Fairbairn 1996). In *G. odontogaster*, sexual selection for long male pregenital claspers has been demonstrated in several natural populations (Arnqvist 1989b, 1992b,c). Finally, pronotal

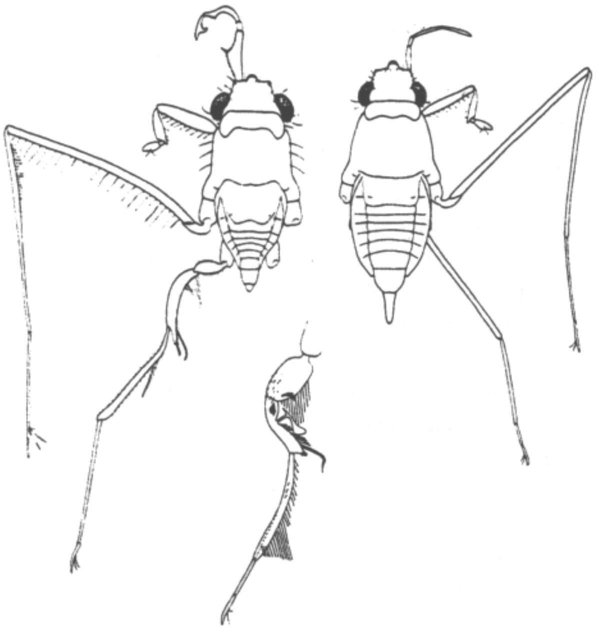

Fig. 8-3. A male (left) and a female (right) of *Rheumatobates rileyi* (reproduced with permission from Andersen 1982), and the left hindleg of a male *Rheumatobates bergrothi* (middle) (after Hungerford 1954). Note the bizarre sexual dimorphism in antennae and hindlegs, as well as the more powerful forelegs of the male.

size, gut parasite load and body mass has been found to be under sexual selection in *G. odontogaster* (Arnqvist 1992c).

Sexual conflict and female choice of male grasping ability

Most evolutionary modifications of male morphology (except body size) investigated so far are designed to grasp females efficiently during mating in one way or another (Andersen 1982, 1990). In a study of *Rheumatobates rileyi* (Fig. 8-3), Silvey (1931) noted that the male antennae were used during mating to grasp the female firmly anteriorly and the hindlegs curved around those of the female thus providing posterior attachment. The relatively powerful and modified forelegs typical of males of most species are adaptations for grasping; the forelegs are used by males during mating to hold the female thorax in a firm grip (Sattler 1957; Andersen 1982, 1989, 1990; Wilcox 1984; Arnqvist 1988, 1989b; Rowe 1992). Further, genitalic modifications in the form of outgrowths and/or processes function to grasp or pinch the female posteriorly (Arnqvist 1989b; Andersen 1991; Preziosi and Fairbairn 1996); the flattened abdomen found in males of many species allows a tighter union to the female (Andersen 1990). It may thus be concluded that there is a variety of male adaptations that serve to increase male grasping ability during mating in water striders. This conclusion is confirmed by the direct observations of sexual selection for traits related to male grasping ability, such as powerful forelegs and long genital processes or segments (Rubenstein 1984; Arnqvist 1989b, 1992b,c; Kaitala and Dingle 1993; Weigensberg and Fairbairn 1995; Preziosi and Fairbairn 1996).

Male grasping traits, which serve to keep the sexes together during mating, are traditionally seen as adaptations to reduce sperm competition by preventing takeovers (Parker 1970, 1984). By grasping a female efficiently, the male avoids being displaced by another male, which may inseminate the same female. However, two lines of evidence strongly suggest that this is not the case in water striders (cf. Thornhill 1984). First, there are no published accounts of true takeovers of mates in water striders. Encroaching males occasionally contribute to the interruption of a mating, but the encroaching male will rarely if ever actually take over the mate; such instances are most likely due to mistaken identity rather than true takeover attempts (Wilcox 1984; Arnqvist 1989b; Rowe 1992; Krupa and Sih 1993). Second, detailed studies of one species suggest that grasping traits have another function (Arnqvist 1989a,b, 1992a,b,c, 1994). The male genital grasping apparatus of *G. odontogaster* has been shown to provide males with posterior attachment to females during the precopulatory struggle. The grasping apparatus is critical for males in enduring the struggle; males with inoperative claspers are easily dislodged by females. Furthermore, males with long claspers are better able to endure female reluctance during the precopulatory struggle, and hence achieve more matings both in the laboratory and in natural populations. In this species, there is sexual selection for long claspers, and female reluctance to mate is thus the mechanism of this selection.

All available information thus suggests that grasping morphologies in water striders are the result of intersexual selection rather than intrasexual selection. Females attempt to dislodge males for reasons of convenience, which selects for male ability to grasp and subdue the females as a side effect. This mechanism corresponds exactly with definitions of sexual selection by female choice, which is typically defined as cases where females have a behavior that tends to bias matings towards certain males (see, for example, Maynard Smith 1987). Male traits that increase grasping ability in water striders should thus generally be seen as the result of female choice for high male persistence during the pre- and postcopulatory struggles (Arnqvist 1992c; Rowe 1994). This is true irrespective of whether the traits function to grasp females during the pre- or postcopulatory struggle, or both.

Given that there is female choice of male grasping ability in water striders, the system corresponds in several ways to a current controversy as to the evolution of female choice. The current view of sexual selection by female choice may be divided into two major schools, with differing views of causes of female mate preferences (see Bradbury and Andersson 1987; Andersson 1994; Johnstone 1995). The 'good genes' school postulates that female preferences evolve under selection for females to mate with ecologically adaptive male genotypes. In contrast, the 'non-adaptive' school holds that preferences evolve for other reasons, and that selection may cause males to evolve maladaptively with respect to their ecological environment. In water striders, females struggle primarily to avoid superfluous and costly copulations rather than to choose males with good genes by testing male vigor (Arnqvist 1992a; Rowe 1992, 1994; Arnqvist and Rowe 1995; but see Weigensberg and Fairbairn 1994), and female choice of male grasping ability thus appear to be a side effect of natural selection acting on female behavior. The characteristics of female choice in water striders parallels those of some other thoroughly studied mate choice systems in frogs, fishes and lizards (Rowe *et al.* 1994).

Secondary sexual traits and coevolutionary arms races

Several authors have proposed that, given sexual conflicts over mating, male and female genitalia and secondary sexual traits may be involved in a coevolutionary arms race (Parker 1979, 1984; Alexander *et al.*, this volume). These hypotheses predict that females should evolve counteradaptations to cope with sexual harassment and gain increased control over matings. Given the conspicuous sexual conflicts in water striders and male morphological adaptations to forcefully grasp females, this group offers ideal systems for studying such mechanical conflicts of interest. For example, the highly modified abdominal spines of *G. incognitus* females have been found to function to reject harassing males: by manipulating the length of these spines, Arnqvist and Rowe (1995) were able to show that the spines increase female ability to dislodge males during the precopulatory struggle, and thus to gain increased control over mating decisions. A number of other traits found exclusively in females are potential candidates for a similar function: females of many species have evolved various sorts of bizarre modifications such as various spines, genital processes and hooks, shortening of the abdomen, and lobes that cover the genital opening (Hungerford and Matsuda 1965; Andersen 1982, 1993; Andersen and Chen 1995). These traits probably also represent 'counteradaptations' that enable females to control matings by making it more difficult for males to establish genital contact; species exhibiting such female traits offer ideal systems to future studies of the coevolutionary dynamics of sexual conflict (Arnqvist and Rowe 1995).

Sexual size dimorphism

Sexual size dimorphism in water striders has been associated with two patterns or processes: allometry for size dimorphism and sexual selection. Comparative studies and phylogenetic analyses indicate that the evolution of sexual size dimorphism in water striders is very complex, but there are no obvious phylogenetic constraints on size dimorphism (Fairbairn 1990; Erlandsson 1992; Fairbairn and Preziosi 1994; Spence and Andersen 1994; Andersen 1994). Even though a number of adaptive mechanisms have been suggested (Andersen 1982; Vepsäläinen 1985; Fairbairn 1990, 1993; Spence and Andersen 1994), direct empirical evidence of sexual selection on body size is scarce and partly contradictory and it is still unclear, for example, why long matings are associated with a high degree of sexual size dimorphism in water striders. Most studies show sexual selection for large males (Sih and Krupa 1992; Fairbairn and Preziosi 1994; Arnqvist *et al.* 1996; Preziosi and Fairbairn 1996; Rowe and Arnqvist 1996). It might be that different mechanisms are interacting in producing apparently conflicting results: Sih and Krupa (1992) and Preziosi and Fairbairn (1996) argued that large males are better able to subdue reluctant females; Fairbairn (1993) suggested that females should allow small males to mate longer due to the costs of loading; and Blanckenhorn *et al.* (1995) suggested that small males may be favored because of lower food requirements. Further, Rowe and Arnqvist (1996) found that small males copulated longer but large males guarded longer in three *Gerris* species. Opposing mechanisms such as these could potentially interact to produce the observed inconsistency and complexity in the effect of male size on mating success between different studies and environmental conditions. At present, it is unclear how sexual conflict and sexual selection contributes to sexual size dimorphism; detailed empirical studies to evaluate this are needed.

Sexual conflict and the intensity of sexual selection

During the past decades, much effort has been spent labeling mating systems of different species. Unfortunately, this has contributed to a somewhat typological view of mating systems, which may have hindered the insights that might be gained from acknowledging that mating systems are plastic and that mating behavior varies with environmental conditions (Zeh and Zeh, this volume). Variability is the hallmark of studies of water strider mating systems; there are few other systems where there is such a thorough understanding of the mechanisms and dynamics of this variability. Recent experimental studies have shown that a number of environmental factors affect various aspects of water strider mating behavior. Factors such as sex ratio, population density, food availability and predation risk all have dynamic effects on female resistance, mating frequency, copulation duration, mate-guarding duration and general mating activity. In a review of the plasticity of water strider mating systems, Rowe *et al.* (1994) showed that most of this behavioral variation can be understood in terms of the sexual conflicts over matings; females seem to 'sample' the rate of male harassment (which in turn is determined by the environment) and adjust their behavior accordingly. These adaptive mating decisions, based on trade-offs between the different costs of mating, can be seen primarily as a variation in the level of female reluctance and as consequences of that variation (Rowe *et al.* 1994).

Mating patterns and sexual selection are population-level manifestations of the sexual behavior of individuals. Because water strider mating systems are so variable, it is not surprising that mating patterns and sexual selection have been found to vary between populations and between different sampling occasions in a given population (Fairbairn 1988; Arnqvist 1989b, 1992c; Fairbairn and Preziosi 1994; Krupa and Sih 1993; Arnqvist *et al.* 1996; Preziosi and Fairbairn 1996). Sexual selection for male size, for example, varies between populations or subpopulations of several species, and there is considerable variation between populations in sexual selection regimes for genital traits related to male grasping ability. There is also a remarkable intraspecific variation in the patterns of assortative mating by size between populations in several species (Fairbairn 1988; Arnqvist *et al.* 1996).

The study of phenotypic selection in natural populations has been given considerable general attention in recent years, and several authors have stressed that a correlational approach is insufficient for inference of causal patterns of selection, and that a more mechanistic approach (i.e. a thorough knowledge of the ecology and behavior of the study organism in concert with studies of selection) may provide new perspectives in evolutionary ecology (see, for example, Endler 1986; Wade and Kalisz 1990; Arnqvist 1992c). In the study of water strider mating systems, the relatively thorough understanding of the mechanisms of selection provides a framework to which we can relate observations of variations in pattern of non-random mating between populations (Sih and Krupa 1992; Krupa and Sih 1993; Rowe *et al.* 1994). It also allows *a priori* predictions about the intensity of sexual selection in different natural populations to be made (Arnqvist 1992b,c, 1994).

The expected variance in reproductive success in males should increase when the operational sex ratio is biased towards males (Andersson 1994). In water striders however, the opposite pattern should be expected since male harassment increases with increased sex ratio, which causes female reluctance and thus the intensity of selection to decrease (Arnqvist 1992a; Rowe 1992, 1994). In accordance with this prediction, Arnqvist (1992b) demonstrated experimentally that the intensity of sexual selection on male claspers in *G. odontogaster* decreased with increased sex ratio, and Krupa and Sih (1993) showed that non-random mating by size in *A. remigis* males was drastically reduced in male-biassed situations. The relation between population density and the intensity of selection in water striders is analogous to that between sex ratio and selection. When population density increases, female reluctance decreases as a result of increased male harassment. In *G. odontogaster*, patterns of sexual selection in natural populations are in accordance with this prediction; sexual selection is relaxed under high-density conditions (Arnqvist 1992c, 1994). The same is true for *A. remigis*, where high-density tended to decrease large male mating advantage (Krupa and Sih 1993). Thus, the predicted as well as the observed relation between sex ratio or density and the intensity of sexual selection in water striders are opposite to general theoretical predictions (Arnqvist 1992b,c; Krupa and Sih 1993; Andersson 1994), which illustrates that a thorough understanding of the mechanisms of selection is essential to predict variations in the intensity of selection and population level effects of such variations (Arnqvist 1994; Zeh and Zeh, this volume).

Because female mating behavior, and in particular female resistance to mating, is affected by a wide range of environmental factors, the intensity of sexual selection should vary accordingly. Results available so far indicate that patterns of non-random mating follow predictions based on our knowledge of female mating behavior. Experimental and observational studies of *A. remigis* have shown that non-random mating by size is also affected by hunger level and predation risk (Sih and Krupa 1992; Rowe *et al.* 1996) as well as by habitat structure (Krupa and Sih 1993).

In conclusion, there is prominent intraspecific variation in mating behavior, mating pattern and sexual selection in water striders. Much of this variation can be understood and even predicted based on our knowledge of the dynamics of sexual conflict, in particular the relation between environment, male harassment rate and female mating behavior.

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