Sexual conflict and the evolutionary ecology of mating patterns: water striders as a model system

Locke Rowe, Göran Arnqvist, Andrew Sih and James J. Krupa

Two core ideas in the study of mating systems and sexual selection are (1) the existence of a conflict between the sexes over mating decisions, and (2) that variation in ecological conditions drives the evolution of adaptive mating strategies and the diversification of mating systems. A recent burst of experimental studies of mating behavior and sexual selection in water striders has focused on the interaction of these ideas and led to new insights into the evolutionary ecology of mating systems and sexual selection.

Locke Rowe is at the Section of Evolution and Ecology, University of California, Davis, CA 95616, USA; Göran Arnqvist is at the Dept of Animal Ecology, University of Umeå, Umeå, S-901 87, Sweden; Andrew Sih and James Krupa are at the Center for Evolutionary Ecology, University of Kentucky, Lexington, KY 40506-0225, USA.

Water striders (Heteroptera) can be seen on the surface of most lakes, ponds and streams (Fig. 1). The ecology and evolution of the group is relatively well-studied[1,2]. During the breeding season, much of their activity is concerned with mating behavior and reflects a dramatic conflict between the sexes (Fig. 2). Even the casual viewer can quickly discern this conflict. Single males chase, grasp and leap upon single females in frantic, but usually futile, attempts to mate. Females flee from this harassment, but if males have successfully gained a purchase on them, a vigorous struggle ensues. These struggles include roles, somersaults and leveraged flips which usually dislodge males. Less often, males endure and females submit to copulation.

On initial examination, the reason for such an open conflict over mating decisions seems simple and invariant. Females store viable sperm for at least 10 days, and there is no direct nutritional benefit of mating for females[10,11]. Therefore, a few copulations over the entire reproductive life of a female will suffice to remove any threat of sperm shortage. Female reproductive success appears to be limited primarily by food shortage and predation risk. Males may similarly be limited by food and predators but they are also limited by the availability of fertilizable eggs. There is a last-male fertilization advantage in gerrids[11,12]; hence, each prolonged or additional mating can be advantageous to males.

Recent research suggests that the degree of sexual conflict and its resolution is anything but invariant! A key to understanding this variation lies in the interaction between female mating behavior, and food and predator limitation. An experimental approach has been used to focus on the underlying conflict between the sexes[13,14] and on how local ecological conditions affect the resolution of this conflict[15–17].

The economics of sexual conflict

Closer examination of the economics of mating reveals that mating is not simply superfluous to females, but is actually costly. Females must carry males during mating and this leads to slower skating speeds[10,18], which, all else being equal, will almost certainly lead to decreased foraging efficiency. Moreover, mating females are at a significantly greater risk of predation than are single females[10,18,19]. For example, Fairbairn[18] showed that the mating female of *Aquarius remigis* was at a greater risk from predation by frogs, perhaps because of increased visibility and decreased mobility. Similarly, attack efficiency of predaceous backswimmers (Notonectidae) is doubled on mating female *Gerris buenoi*[19], compared to solitaries.

Given a lack of benefits and several costs of mating to females, it is clear why they are generally reluctant to mate. Yet, females mate much more often than the few times required for full fertility. In fact, remaining single (resisting) in the face of repeated harassment by males can be even more costly than mating itself. Fleeing from males may displace females from prime foraging areas and otherwise occupy their time. Wilcox[20] has shown that foraging success of single females declines significantly in the presence of harassing males. Furthermore, if a male successfully grasps a female, she must struggle to disengage from him. The struggles appear to be energetically costly and they dramatically increase the risk of predation to females[19]. Thus, in females there are energetic and mortality costs of both mating and remaining single. Adaptive female mating behavior must somehow balance these costs (Box 1). Females act to balance these costs by varying their reluctance to mate (e.g. struggle duration) and the intensity or duration of these struggles is a measure of this reluctance[21–23].

Male harassment and adaptive female mating decisions

Because harassment is costly to females and is directed primarily towards single females, increased harassment is expected to lead to decreased reluctance of females to mate and, therefore, increased mating activity (Box 1). Increased mating activity (proportion of time spent mating) may be accomplished either by an increase in mating frequency, an increase in mating duration, or both. In a series of experiments, environmental variables expected to affect harassment rate (e.g. density, sex ratio) have been manipulated to test the prediction that female reluctance is a declining function of male harassment rate. As predicted, in *G. buenoi*, a more male-biased sex ratio was associated with increased per capita harassment rates, decreased female reluctance, and, as a result, an increase in the probability of mating per attempt and increased mating frequency[21]. Similarly, in *Gerris odontogaster*, females were less reluctant to mate in conditions with either a more male-biased sex ratio or a higher overall density[23]. An observational study suggests that a more complicated relationship between harassment rate and female reluctance may occur in *A. remigis*[22].

Experimental manipulations have also shown that male-biased sex ratios lead to increased mating duration, as expected from adaptive female behavior[21–24]. Yet sex ratio is expected to affect optimal mating duration from a male point of view as well. A more male-biased sex ratio is associated with a higher probability of sperm displacement by a subsequent male, and a lower probability of locating a new single female. Therefore, careful experiments are required to distinguish the contribution of each sex to the determination of guarding duration (Box 2). Neither sex appears capable of forcing the other to stay in tandem. Thus, guarding duration is expected to be determined by whichever sex has the shorter optimum.

An alternative way for females to avoid harassment by males is to reduce their detectability by males (e.g. hide). In *A. remigis*, when males are present, females tend to spend more time on or near the shoreline, rather than foraging in centre areas where harassment rates are high[20,29]. Thus, in situations where refuge from male harassment is present, male-biased sex ratios may not lead to the expected increase in mating frequency[30].

Food and mating behavior

Effects of food availability on mating frequency depend on how feeding *per se* influences mating behavior and how hunger affects mating behavior. Though there has been some evaluation of the former effect[21], most concerns the latter. Several experimental studies suggest that hunger has little effect on mating behavior of males[3,21,31]. Effects of food availability on female behavior and, in particular, female reluctance to mate should depend on the effect of mating on female feeding efficiency. If mating females enjoy higher feeding efficiency than single females, then hungry females should be less reluctant to mate and low food availability should be associated with high mating frequency. If, however, mating females have lower feeding rates than single females, then the opposite predictions should hold. Interestingly, both scenarios may occur in gerrids.

In *A. remigis*, mating females are not harassed as intensively by males as solitary females are[20,28,29]; as a result, they enjoy higher feeding rates[20]. Therefore, hungry females are expected to be more willing to mate than satiated females. However, experimental evidence offers little support for this prediction. Clark[24] found no effect of female hunger on mating duration and did not measure mating frequency. Reduction of food availability for both sexes simultaneously (and presumably hunger) resulted in no significant effect on mating frequency, and contrary to prediction, decreased mating duration[32]. One possible explanation is that males, which do not feed during mating, abandoned females because of encroaching hunger. To evaluate this hypothesis would require separate manipulations of both male and female hunger levels.

In contrast to *A. remigis*, mating female *G. buenoi* are usually inactive, typically resting on emergent vegetation and rarely foraging[21]. Because there is no apparent advantage of mating to foraging females and there is a cost (predation risk, speed, etc.), females are expected to be less

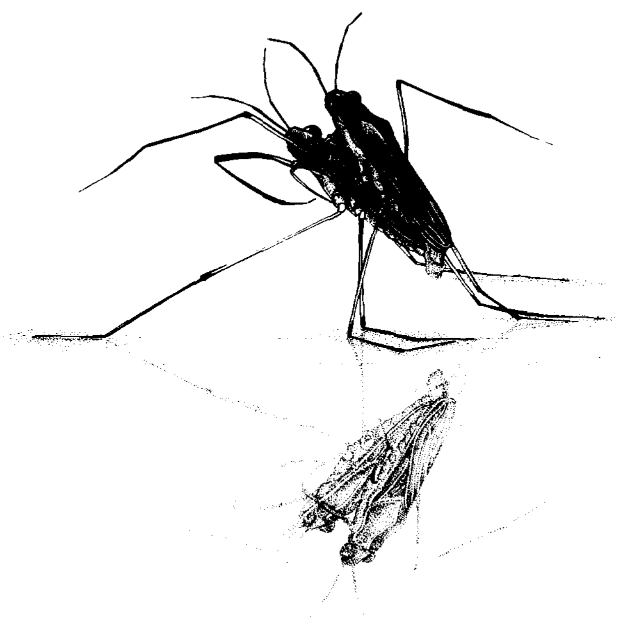


Fig. 1. A pair of water striders (*Gerris odontogaster*) involved in a premating struggle. The female is raising her midlegs, and the couple will flip over backwards. She simultaneously tries to loosen the male's grasp with her forelegs. This behavioral sequence ('backwards somersaulting') is performed repeatedly and is a major component of female reluctance behavior. *Illustration by Görel Marklund.*

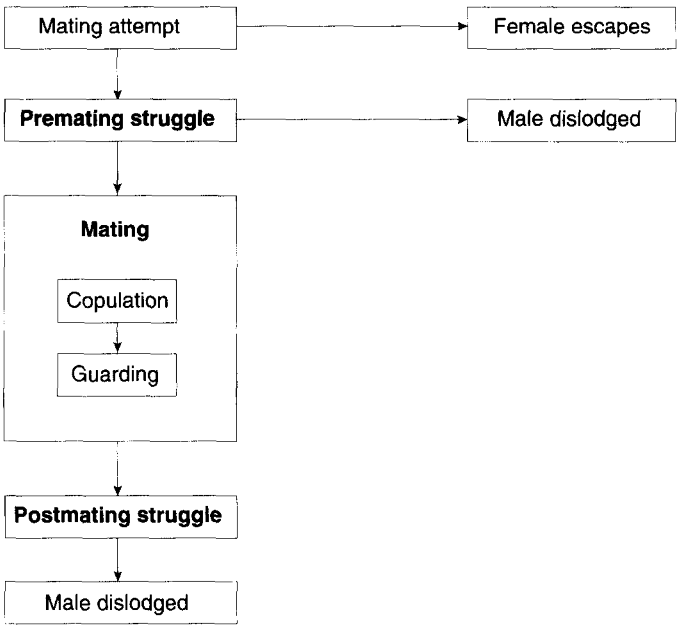


Fig. 2. The mating sequence: arrows connect each subsequent event in the mating sequence. We refer to mating attempts by males as harassment, mating as the combination of copulation (sperm transfer) and mate guarding, which is often very long relative to the copulation phase. Throughout the mating phase, males ride on top of females. Mating usually begins and ends with a struggle initiated by the female. In some species (e.g. *G. buenoi, G. odontogaster*), the distinction between copulation and mating phases is clear because males withdraw their adeagus (intromittent organ) at the switch point, while in *A. remigis* the adeagus remains inserted in the female throughout the mating period. The sequence shown here is a composite view of observations on several species in the genera, *Aquarius* and *Gerris* (e.g. *A. remigis, G. buenoi, G. incognitus, G. lacustris, G. lateralis* and *G. odontogaster*). However, even within these species, mating behavior is nontypological. Moreover, other distinct mating sequences occur within other gerrid species including those with intra- and intersexual surface-wave signalling, which have intriguing implications for conflict resolution within and between sexes, and even among species (e.g. Refs 3–8; reviewed in Refs 2,9).

willing to mate when they are hungry. Mating durations appear too short (from a few minutes to a few hours) to increase male hunger to the point where it would pay to abandon females. Separate manipulation of male and female hunger levels demonstrated that in accordance with prediction, hungry females mated less frequently than well-fed females and male hunger had no effect on either frequency or duration of mating[21]. However, contrary to prediction, there was no effect of female hunger on mating duration.

Movement patterns

Given that various ecological factors influence costs and benefits that govern male and female mating behaviors, and given that these ecological factors vary in space and time, we expect males and females to show movement patterns that respond to this spatiotemporal variation. Recent studies on water striders have been among the few to use experiments to examine this issue in the context of mating systems. Nummelin[31] reduced local food availability in a Ugandan stream and found that female, but not male, gerrids increased their dispersal tendency from that area. When females were subsequently removed, males left the area. The implication is that females follow food, while males follow females. Similar patterns, with an additional effect of habitat structure appear in *A. remigis*[33]. Males tend to accumulate in areas with relatively few sites for females to escape harassment. These 'hot spots' were characterized by high density, a male-biased sex ratio and a high female-mating frequency. When additional refuge for females was added (thus reducing female availability to males), males tended to leave these sites and move to other 'hot spots'.

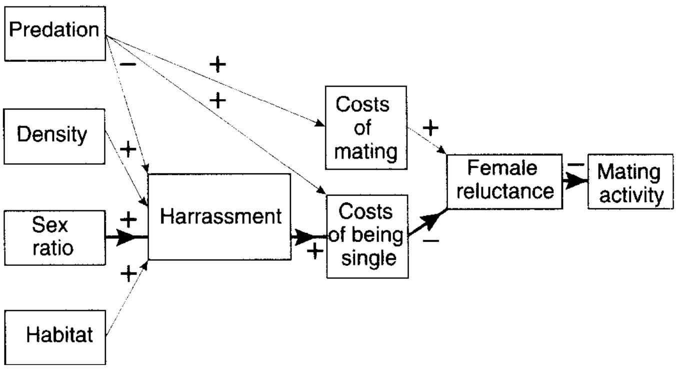
Sexual selection as a side effect of natural selection on female mating behavior

Studies of sexual selection typically focus on pattern rather than process, and one consequence is that the mechanism of selection often remains obscure[34,35]. In gerrids, recent studies have disclosed some of the proximate and ultimate mechanisms of sexual selection. These studies have shown that adaptive female reluctance to mate selects for certain male phenotypes. Therefore, female choice may be best understood as a side effect of natural selection acting on female reluctance.

Males of several species of water striders possess a variety of structural features which serve as grasping devices during mating[36–38]. In *G. odontogaster*, males are provided with abdominal claspers which enhance the grasp of females by males. Since takeovers of mating females by other males do not occur, claspers are unlikely to function in male–male competition[37]. Instead, claspers are critical for males to endure female resistance during premating struggles. Males with longer claspers have a greater probability of enduring female resistance, and sexual selection for long male claspers has been documented in laboratory experiments and in direct measurements of selection in the wild[37,39]. Therefore, female resistance biases the mating frequency of males according to clasper size, and clasper size is thus, by definition, under sexual selection by female choice[40]. The existence of male structures with apparently similar function in several other gerrid species suggests similar evolutionary histories. Other components of male size may similarly be related to their ability to subdue females, and nonrandom mating by body size[33,41–44] and leg size[4,28] has been found in several species.

Box 1. Convenience polyandry

This figure shows how environmental variables affect the costs of mating and the costs of remaining single. Female reluctance to mate (and hence their mating activity) reflects an adaptive balance of these costs. The relative ease with which experiments can be conducted on gerrids has facilitated the identification of each path and tests of the predicted consequences of combined paths on mating activity. For example, under male-biased sex ratios, harassment of females is increased. Because harassment is directed primarily towards single females and is costly, the costs to females of remaining single increase. Females respond to these increased costs by decreasing their reluctance to mate and mating activity increases. This pathway is highlighted in the figure and discussed further in the main text.



The path diagram emphasizes three main points. First, sexual harassment of females by males plays a central role in determining the optimal mating activity of females: most pathways pass through the harassment box. In the absence of harassment, females should mate only rarely to replenish sperm supplies. Thus, it is costly harassment by males that leads to adaptive multiple mating by females. This sort of multiple-mating system is aptly termed Convenience Polyandry[17,21,22]. Second, several potentially variable components of the environment have direct and indirect effects on the economics of female mating activity. Moreover, some known environmental effects (e.g. hunger; see text) and other unknown variables could be included in a more-complete model. Thus, we expect high spatial and temporal variation in mating patterns. Finally, predation has effects on optimal mating activity of females that are potentially complex and difficult to predict. This results because predation has positive effects on both the costs of mating and the costs of remaining single, as well as negative effects on harassment rates (see also Box 5).

Box 2. Accounting for female interests in the resolution of sexual conflicts

Several authors have recently emphasized the lack of focus on the interests of females in mating systems and sexual conflict[25,26]. Yet such a focus has a relatively long history in research on insect mating systems[27], including those of gerrids[20,21,28]. Recent studies on gerrids have explicitly considered the economics of mating for females and their adaptive responses to experimentally varied environments (see Box 1 and text).

In gerrids, the two most striking manifestations of conflict are pre- and post-mating struggles, and experiments demonstrate that females play the pre-eminent role in determining their outcome. Variation in female reluctance to mate (e.g. duration of premating struggles) is best explained by adaptive female behavior rather than male[21–23]. Even when males are experimentally induced to be more persistent in premating struggles, females are able to foil their attempts with equal success[22].

In most gerrid species, neither sex appears able to force the other to remain in tandem. One possible exception is in species where large males carry small passive females beneath them[1]. The relative influence of males versus females in determining mating duration can be evaluated by three methods: (1) by direct observation of postmating struggles; (2) by manipulating conditions that yield opposite predicted changes in mating durations for males and females; and (3) by independently manipulating conditions for each sex. Direct observations show that, in some situations, guarding is always terminated by female-initiated struggles, but in others, both males and females appear to terminate matings[21,22]. Experimental results suggest that both males and females terminate matings and that their relative roles vary among species and environmental conditions.

Box 3. Origins of sexual selection in gerrids: analogies with sensory exploitation

The characteristics of sexual selection by female choice in water striders parallels those of some other thoroughly studied mate-choice systems in frogs, fishes and lizards[45-47]. Three important and general insights can be gained.

First, a common feature of all these mating systems is that the basis for female mating preference appears to have evolved before male traits, since female mate preferences are found in several related species within monophyletic groups whereas male traits are found only in some species. Female resistance occurs in virtually all species of water striders but specific, male grasping traits have evolved in only a subset, suggesting that this common feature holds true for water striders as well.

Second, male traits have apparently evolved to match the pre-existing female mating preferences (an evolutionary pathway termed 'sensory exploitation'). Some of the morphological traits of water striders are obviously designed to grasp females efficiently, and in one species, male traits have been shown to function in the context of matching/overcoming female resistance.

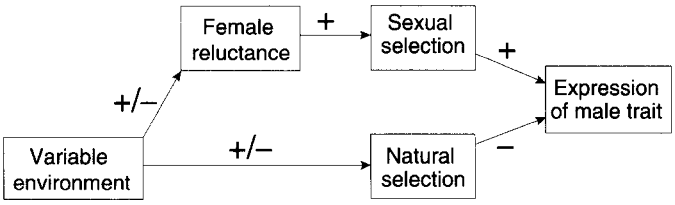
Third, in all these systems, female mating preferences are under natural selection, and the evolution of male traits via female choice appears to be a side effect of this phenomenon[45]. This is the case in water striders, where female resistance is adaptive in terms of natural selection (balancing predation risk, feeding ability, etc.), and female choice of male grasping traits in some species is most likely a secondary side effect[19,39]. For water strider mating systems, there is a mechanistic understanding of the reasons for, and the nature of, natural selection acting on female mate preferences.

Box 4. Variable selective regimes in *Gerris odontogaster*

Mating dynamics and sexual selection in water striders are extremely variable. Female mating behavior determines the intensity of sexual selection, and female mating behavior is affected by a number of different environmental factors (Box 1). Thus, there is a complex and dynamic relationship between the environment and the selective regimes of local populations.

This microevolutionary scenario has been studied in detail for a male grasping trait in the water strider *G. odontogaster*. In this species, female resistance to mate selects for long abdominal claspers in males[37]. Further, as population density increases, females become less-resistant[23] and the relative importance of long claspers decreases[49]. Sexual selection should thus be negatively density dependent. Direct measurements of selection in natural populations confirm this prediction[39].

However, there are also costs associated with long claspers. Claspers appear to interfere with the molting process, and the longer the claspers the higher the risk of mortality due to inter- and intraspecific predation during molting[50]. Thus, there is natural selection against long claspers, and this selection is positively density dependent. Sexual and natural selection on this trait are, therefore, agonistic and the combined effects (net selection) on clasper length thus depend on population density. A schematic view of how environmental variables may affect both sexual selection (as a side effect of adaptive female reluctance) and natural selection on male secondary traits is shown below.



In contrast to general theory, which assumes that sexual and natural selection should balance, net selection thus should be zero only rarely, since both sexual and natural selection vary with density. Rather, local net selective regimes should range from positive to negative values depending on environmental conditions and the trait should be in a state of evolutionary flux rather than at equilibrium. Local populations vary with respect to length of claspers and mean trait value decreases with increasing population density, indicating that population density is a major environmental determinant of local selective regime in natural populations[50].

Since the mechanism of female choice (female resistance) is well-understood in some gerrids, these can be used to disentangle hypotheses for the evolution of female preferences. Premating struggles by females may evolve for two principal reasons: (1) as a side effect of a general reluctance to mate; or (2) as a means of selecting mates of superior quality[21-23]. Empirical as well as theoretical treatments of this problem strongly support the view that female resistance is governed by factors related to direct natural selection on female reluctance rather than adaptive mate assessment (choice of mates with good genes)[10,19,21-23,33]. Although both hypotheses are compatible with increased mating frequency under male-biased sex ratios, only the general reluctance hypothesis predicts that females will become less-reluctant to mate under such conditions. All manipulations of sex ratio in gerrids support the general reluctance hypothesis (see above and Box 1) and thus indicate that sexual selection associated with female reluctance represents a side effect of natural selection acting directly on female resistance. It remains possible that a more active form of choice may also be occurring in gerrids, but experimental evidence is lacking. Although details of female choice in gerrids are specific, the general features of the system bear close resemblance to those of some other mate-choice systems (Box 3).

Spatial and temporal variation of sexual selection

Accounting for spatial and temporal variation in sexual selection is a major challenge (e.g. Ref. 48). Considering the tremendous plasticity of gerrid mating behavior, it is not surprising that intraspecific variation is the hallmark of field and laboratory investigations of patterns of sexual selection. Understanding this variation requires an accounting of variation in the main behavioral component that shapes mating patterns in gerrids – female reluctance to mate. Female reluctance is predicted to be a declining function of rates of male harassment, and harassment is a function of various environmental factors (Box 1). Field measurements of sexual selection in *G. odontogaster* corroborate this link with harassment; the intensity of sexual selection on a number of traits has been shown to decrease with male-biased sex ratios and has been found to be highest under low-density conditions[39,49] (Box 4). Patterns of non-random mating in *A. remigis* also vary in accordance with predicted variations in female reluctance[30,33]. In this species, large males are thought to have a greater ability to overcome female resistance, and the degree of large-male mating advantage has been found to be negatively related to the rate of male harassment of females (Box 5).

Since water strider females respond adaptively to environmental factors by altering their resistance to mate, the variability of sexual selection may again be seen as a side effect of variations in factors affecting female mating decisions. Sex ratio, population density, food abundance and predator presence have all been shown to affect female mating behavior, but other factors such as microhabitat structure, temperature and the density of other water strider species, as well as interactions between these factors, may be equally important. The picture that emerges from recent studies of the evolutionary ecology of water strider mating systems is interesting in that it is dynamic and non-typological. Local populations or even subpopulations have different sexual selection regimes and thus form spatial microevolutionary mosaics, where the prevailing nature of sexual selection is determined by the local environmental conditions[39,44,50] (Box 4). Such spatial and temporal variability in selection may be of large evolutionary importance, since it should promote the maintenance of both intra- and interpopulational genetic variation in water striders.

Box 5. Predation risk and mating behavior

Although adult water striders appear to suffer from relatively little predation *per se*, predation risk may nonetheless influence every stage of the interaction between male and female gerrids. These effects are particularly well-studied for the stream water strider (*A. remigis*) and its potential predator, the green sunfish (*Lepomis cyanellus*)[32,33].

Sunfish are most likely to attack gerrids that are active in the centre of pools. The presence of sunfish thus causes a drastic reduction in the activity of both male and female *A. remigis*. This results in a decrease in encounter rates between males and females, which tends to reduce mating frequencies. This effect is not surprising: faced with an important competing demand – the need to avoid predators – water striders reduce their mating activity.

Predation risk also influences patterns of non-random mating, in this case, in surprising and potentially complicated ways. In the absence of sunfish, larger males enjoy slightly higher mating success than smaller males. In the presence of sunfish, however, the large-male mating advantage (LMMA) is significantly increased. This goes against the predictions of recent models of female mate choice[51], but fits the view that adaptive variation in female reluctance determines LMMA. A mechanism that is consistent with observed results is that predation risk causes a reduction in male–female harassment rates that favors increased female reluctance to mate and thus an increase in the LMMA.

Finally, predation risk has strong effects on mating duration. Again, several mechanisms could explain this pattern. Because mating can be risky, from both a male and a female view, the presence of predators should cause a reduction in mating duration. The exact mechanism can involve either direct physical interference (i.e. an actual attack causes males and females to separate as part of an escape attempt), or behavioral shifts (males or females terminate mating earlier without an actual attack). Behavioral shifts could represent a response to risk *per se*, or to increased hunger associated with predator avoidance. Regardless of the mechanism, reductions in mating duration may have important effects on the dynamics of sperm competition in this system.

Conclusion

Recent experimental studies on water striders have provided an unusually detailed understanding of a plastic mating system. The emerging view is that variable ecological factors (e.g. density, sex ratio, food availability, predation risk) set the costs and benefits for each sex that govern the dynamics of sexual conflict, and thereby determine mating patterns. Mating patterns, in turn, produce patterns of sexual selection that can explain the evolution of sexually dimorphic traits. These results point to the value of combining experimental studies of process with observational studies of pattern. Future studies using this approach will yield valuable insights into the evolutionary ecology of mating systems.

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