Behavioral Ecology Vol. 7 No. 4: 474–479

An experimental test of condition-dependent mating behavior and habitat choice by water striders in the wild

Locke Rowe, James J. Krupa, and Andrew Sih
Center for Evolutionary Ecology, University of Kentucky, Lexington, KY 40506-0225, USA

Individual condition is expected to be an important determinant of many behaviors, including mating dynamics and habitat choice. In this study we experimentally investigated the linkages between individual condition, habitat use, and mating dynamics in the wild. We manipulated recent feeding history of the water strider, *Aquarius remigis,* and then quantified the habitat use and mating activity of males and females. Females could choose from three habitats (refuge, near shore, and open). On the water surface (open and near-shore habitats), in contrast to refuge, females can forage, but they are exposed to predation and sexual harassment by males. We tested three main hypotheses. First, we predicted that single females that were fed, relative to those that were not, would reduce their exposure to predators and male harassment by increasing their use of refuge. Similarly, we predicted that fed females that were mating would spend more time in refuge than those that were not fed. Our results support these two predictions. Fed single and mating females significantly increased their use of refuge. Third, we predicted that mating activity (proportion of time spent mating) of fed females would be reduced relative to starved females, because of reduced exposure to males while in refuge, and perhaps because of decreased receptivity to male mating attempts while on the water surface. Mating activity of fed females was about one third that of starved females. The decrease in mating activity could not be accounted for by any change in female receptivity, but could be accounted for by change in habitat use. The decrease in mating activity may have resulted from decreases in both mating frequency and mating duration. Our estimates of minimum mating frequency indicate a large and significant decrease, but we were unable to assess mating duration. We found no significant effect of our manipulation on habitat use or mating activity of males. *Key words:* condition, habitat choice, hunger, mating, water strider. *[Behav Ecol 7:474–479 (1996)]*

There is an increasing recognition that the behavior and life history of an individual depends, in often complex ways, upon that individual's current condition (e.g., hunger, energy stores, parasite load, etc.). Individual decisions that are expected to be condition-dependent include diet choice, habitat choice, reproductive allotment, development of secondary sexual traits, and life-history transitions (Crowley et al., 1991; Houston et al., 1993; Ludwig and Rowe, 1990; Mangel and Clark, 1986, 1988; Mangel and Ludwig, 1992; McNamara and Houston, 1986; Nur and Hasson, 1984; Price and Liou, 1989; Price et al., 1988; Rowe and Ludwig, 1991; Rowe et al., 1994b). The dependence of mating dynamics upon individual condition has received relatively little attention, but may offer an explanation for much of the variation in mating dynamics among individuals, populations, and species.

In systems that include direct nutritional benefits of mating to females, females in poorer condition may accept or solicit mating more frequently (Gwynne and Simmons, 1990; Thornhill, 1976). An alternative and perhaps more general mechanism by which condition may affect mating behaviors is through habitat choice and foraging behaviors. Here, no direct nutritional contribution from male to female is required. Choice of habitat by individuals has been shown to depend on hunger level (Dill and Fraser, 1984; Godin and Smith, 1988; Milinski and Heller, 1978; Pettersson and Brönmark, 1993), and habitat use is linked to mating dynamics in several species. For example, localized resources may lead to aggregation of females and (perhaps in response) males, resulting in high mating activity (Bradbury et al., 1986; Parker, 1978; Vehrencamp and Bradbury, 1984; Westcott, 1994). We report here results of experimentally manipulating the condition of individuals in the wild to test hypotheses concerning the linkages between condition, habitat choice, and mating dynamics.

Water strider mating behaviors provide a relatively rare system in which the effects of hunger, feeding, and habitat choice on mating dynamics has been a central theme (Clark, 1988; Lauer, 1995; Rowe, 1992; Rubenstein, 1984; Sih et al., 1990; Spence and Wilcox, 1986; Wilcox, 1984). In water striders, most mating is superfluous and costly to females, and these costs are imposed by males. Females store sperm and males appear to provide no nutrition to females, yet females mate repeatedly. In many species, males vigorously harass single females, and females usually actively repel or otherwise avoid these mating attempts (for reviews, see Arnqvist, in press; Rowe et al., 1994a; Spence and Andersen, 1994). Resulting struggles dramatically increase predation risk to both sexes and appear to be energetically costly (Rowe, 1994). However, mating itself is also costly to females. Males ride passively on the backs of females during mating, which may last several hours. In the absence of male harassment, mating females are at increased risk of predation, skating speed is reduced, and foraging is less efficient (Arnqvist, 1989; Fairbairn, 1993; Rowe, 1994; Wilcox, 1984). Thus, in the presence of males, females must balance the costs of mating with those of harassment (Arnqvist, 1992; Rowe, 1992).

Alternatively, females may avoid males altogether. In stream-dwelling species, there is strong evidence of behavioral avoidance of males by females. Single female *A. remigis* actively avoid male harassment, and the increased predation associated with open water, by hiding along the shoreline or otherwise seeking refuge (Krupa et al., 1990; Sih et al., 1990; Wilcox, 1984). Yet such avoidance mechanisms carry a cost. Foraging opportunities are greater in the open water (Rub-

---

L. Rowe is now at the Department of Zoology, University of Toronto, Toronto, Ontario M5S 1A1, Canada.

Received 24 January 1995; accepted 7 December 1995.

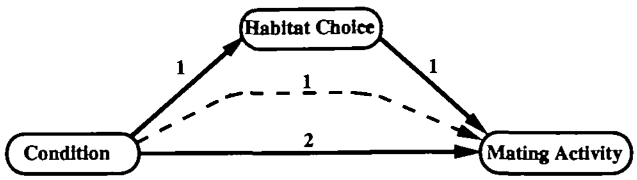

Figure 1
A path diagram showing the potential direct (solid lines) and indirect (dashed lines) linkages between condition (hunger), habitat choice (use of refuge), and mating activity. Two possibly complementary pathways are (1) hunger leads to decreased use of refuge, and use of refuge decreases mating activity and (2) hunger leads to increased mating activity. In both cases, hunger leads to increased mating activity, but through alternative pathways. In the first case (paths are labeled 1), the path is indirect, and in the second case (path labeled 2), the path is direct.

enstein, 1984; Wilcox, 1984). Thus, female habitat use and mating behavior may reflect a balance between foraging needs, predator avoidance, and the costs of male harassment. Rubenstein (1984) and Wilcox (1984) suggested that female *Aquarius remigis* foraging in the open water may mate to decrease harassment by males and thus increase their foraging success. Gerrids forage on dead and trapped insects on the water surface; in stream pools the flow of prey is greatest at the site of flow into the pool. Foraging females jockey for position in these areas. However, constant harassment by males may displace females from these prime foraging spots and decrease their prey-capture efficiency (Wilcox, 1984).

Several predictions about condition-dependent mating behavior in *A. remigis* can be derived from the hypothesized linkages with female foraging and habitat use. First, we expect well-fed single females to spend more time in refuge than hungry single females, given that foraging entails predation risk to females (a cost that is compounded for single females by male harassment and mating). This is a general prediction from condition (or state)-dependent foraging theory (Ludwig and Rowe, 1990; Mangel and Clark, 1986, 1988; McNamara and Houston, 1986). For individuals in relatively good condition, marginal gains in reproductive output for improving their condition are low. Similarly, we expect well-fed females that are mating to forgo foraging and increase their use of refuge. Finally, we expect mating activity of hungry females to increase relative to that of satiated females. This may come about through two, possibly complementary, mechanisms. First, if females accept costly matings in return for reduced harassment and hence increased foraging efficiency, then hungry females should be more willing to mate than well-fed females because the advantages of foraging are increased. This scenario suggests a direct link between the condition of females and their mating dynamics (Figure 1). Alternatively, mating frequency of hungry females may increase in spite of a constant reluctance to mate. Hungry females may mate more simply because they spend more time foraging and are hence exposed to a greater rate of harassment. This latter scenario suggests direct linkages between condition and habitat use and between habitat use and mating behavior, but only an indirect linkage between condition and mating behavior (Figure 1).

The dependence of male habitat choice on hunger is more difficult to predict because refuge use decreases the benefits from both feeding and mate acquisition. If foraging needs dominate male behavior, then well-fed males may similarly reduce risky foraging and increase refuge use. Hunger may also decrease mating activity of males because it conflicts with foraging: unlike females, males cannot feed and mate simultaneously. However, if mate acquisition dominates male behavior, than we expect no effect of feeding history on male habitat use or mating behavior.

Food manipulations have had variable effects on mating behaviors of *A. remigis* (Clark, 1988; Lauer, 1995; Sih et al., 1990). Clark (1988) found no difference in the mating duration of hungry compared to fed *A. remigis*. However, he did not measure mating frequency or mating activity (percentage of time spent mating), both of which may have increased in hungry females. Sih et al. (1990) found that when both males and females were deprived of food, mating activity and mating duration were decreased. These results are difficult to interpret in the present context because both sexes were simultaneously deprived of food. Lauer (1995) found no effect of female hunger on reluctance to mate but did not allow simultaneous habitat choice. In addition, all of these studies were conducted in the laboratory where the benefits of mating to females (decreased harassment and increased foraging efficiency) may differ from those in the wild. To directly test our predictions, we altered the hunger state of females and males independently and subsequently followed their habitat use and mating behavior in the wild.

METHODS

Experiments were conducted in the spring of 1993 at Bathrobe Creek, a tributary of Boone Creek, near Lexington, Kentucky, USA. At this time of year the pool is typically inhabited by 25–40 adult *A. remigis,* as well as a few larval *A. remigis*. The pool (3 × 12 m) is bounded by a shallow waterfall upstream and a riffle zone downstream. The complete water surface and stream banks are observable from the stream bank. All observations were made from the stream bank by two observers with binoculars.

On each of 4 days (=dates=replicates), we attempted to collect all adult gerrids from the pool. Sixteen males and 16 females were then randomly assigned to each of two treatments (8 fed and 8 unfed of each sex), and any extra gerrids were moved downstream. On some days there were not enough gerrids to fill the treatments. On these days we collected the required additional gerrids within a few meters up- or downstream. Experimental gerrids were color-marked on their dorsal pronotum and abdomen according to sex and treatment. Females were given additional marks on their midleg femurs so that they could be identified while mating. Because we conducted replicates, sequentially at the same site, individual gerrids were often reused (approximately 30% per date). To reverse the possible bias introduced by individuals appearing in same treatments in more than one replicate, and to remove any bias of color of mark, we reversed colors assigned to each treatment on each subsequent day.

We placed marked gerrids in one of four streamside wading pools (1.6 m diam) according to sex and treatment. Pools contained stream water to a depth of 3–5 cm and pieces of styrofoam for gerrids to rest upon. Sexes were held separately to remove any effect of the interaction of males and females during the treatment period that may have carried over to the observation period. In the "fed" treatment, gerrids were provided with an abundant supply of previously frozen crickets and/or assortment of recently collected and killed terrestrial insects. Both males and females readily fed on the food we provided. The "unfed"-treatment gerrids were given no food. The treatment period lasted for 2–3 h. This period of time is sufficient to increase nutritional condition in these bugs. Jamieson and Scudder (1977) report that adults feed to satiation in 2–2.5 h, following 48 h of starvation. Both the feeding regime and duration were consistent between sexes and treatments on each day.

After the treatment period, we released gerrids into the

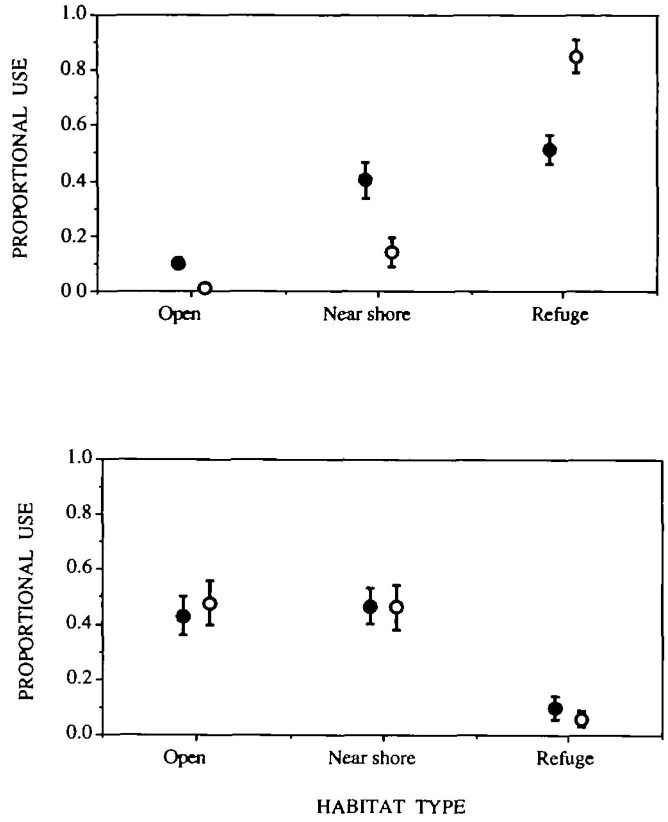

Figure 2
Mean (±SE) habitat use of fed (open symbols) and unfed (filled symbols) single females (top panel) and males (bottom panel).

stream. Within 15 min we began the observation period. At 10- or 15-min intervals we carefully scanned the water surface and stream banks to locate gerrids. Each sighting was scored for sex, treatment, mating status (mating or single) and habitat ("refuge," out of the water on the stream bank; "near shore," within 10 cm of the shoreline; and "open water," >10 cm from shore). The observation period lasted 1–1.5 h. The interval of observations and the total observation period were consistent between sexes and treatment on each day.

For each date we calculated the following variables for each sex and treatment: (1) the proportion of observations in which individuals were mating (mating activity); (2) the proportion of observations of pairs that occurred in each of the three habitats (we confined this variable to females because it is the female that propels mating pairs); (3) the proportion of observations of singles that occurred in each of the three habitats; and (4) the proportion of the total population that was resighted (resighting efficiency).

There were strong effects of date on behavior; therefore, we analyzed the data with paired *t* tests to compare means where means were paired by date. Our main interest was to contrast the switch from habitats where feeding and harassment occur (open water and near-shore zones) with refuge, where neither feeding nor harassment occur. Therefore, we reduced the number of potential comparisons and thus increased the power of tests by comparing the effect of feeding only on refuge use, rather than on all three habitats. Any change in refuge use must be reflected in a decrease in the sum of open water and near-shore habitats. We used one-way tests for our a priori hypotheses (female behavior) and two-way tests for any tests without a priori hypotheses (male behavior). All proportions were arcsine transformed before analysis.

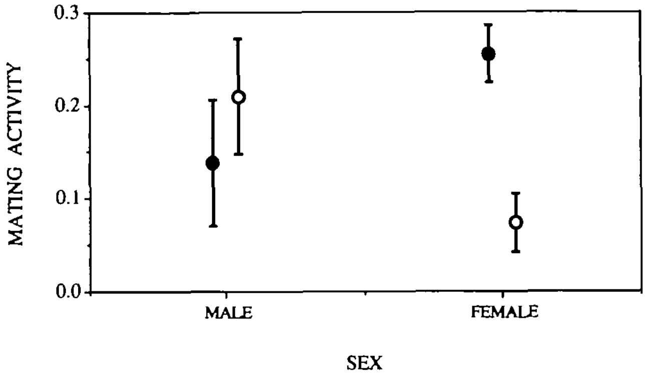

Figure 3
Mean (±SE) mating activity of fed (open symbols) and unfed (filled symbols) mating females.

RESULTS

General behavioral observations

Our qualitative observations of the behavior of *A. remigis* were similar to quantitative and qualitative observations reported earlier (Krupa et al., 1990; Rubenstein, 1984; Weigensberg and Fairbairn, 1994; Wilcox, 1984). Females that were skating in the open water (presumably foraging) were harassed repeatedly by males. Females were reluctant to mate with these males, and hence struggles ensued if a male successfully grasped a female. As a result, matings typically began in the open water, but also in the near-shore zone. In contrast to females in the open water, those in the near-shore zone were less active and were harassed less frequently. Males in the near-shore zone appeared to be tracing the shoreline in search of females and would attempt to mount those that were detected. Females in refuge were inactive and were not harassed. Although we saw only several initiations and terminations of mating, all initiations occurred on the water and included a premating struggle, and all matings terminated with a postmating struggle.

Effects of feeding on habitat use and mating activity of females

Experimental feeding had strong effects on habitat use of single and mating females. Fed single females increased use of refuge and decreased use of both open and near-shore habitats (Figure 2a). Unfed single females spent about 50% percent of their time on the water surface (near-shore and open-water habitats) where foraging is possible, and about 50% of their time in refuge. In contrast, fed single females spent almost 90% of their time in refuge. The shift of fed females to the refuge was reflected in a significant increase in refuge use (t = 6.328, df = 3, $p < .005$).

Mating activity of unfed females was nearly three times that of fed females (t = 3.2, df = 3, $p < .03$; Figure 3). Most of the mating activity of unfed females occurred out of refuge, and in contrast, most of the mating activity of fed females occurred in refuge (Figure 4). We expect that most or all matings started on the water. Thus, like single fed females, mating fed females tended to increase their use of refuge and decrease their use of both near-shore and open-water habitats. The increase in use of refuge was significant (t = 3.31, df = 3, $p < .05$).

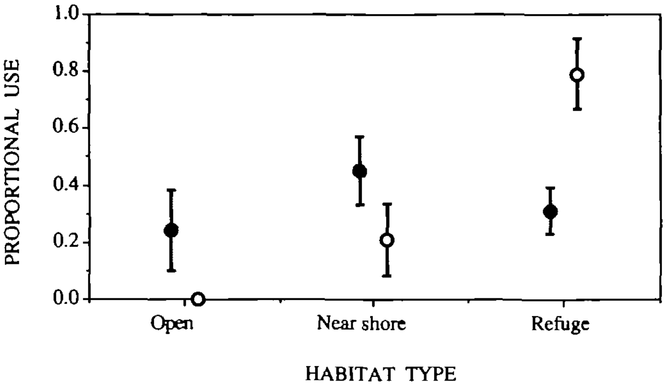

Figure 4
Mean (±SE) habitat use of fed (open symbols) and unfed (filled symbols) mating females.

To determine whether females out of refuge were more likely to mate if hungry, we compared the proportions of the total number of females in the open-water and near-shore habitats that were mating in hungry and recently fed treatments. Among hungry females, 49 ± 0.02% (SE) in these habitats were mating compared to 40 ± 0.11% (SE) of recently fed females; there is no significant difference between these means (t = 0.80, df = 3, p = .5).

Because each sex was not marked individually, but only according to class, we cannot determine how much of the decrease in mating activity of fed females resulted from a decrease in mating frequency or from a decrease in duration of individual matings. However, we can estimate the minimum number of matings by counting the number of new color combinations of pairs at each observation period for each replicate experiment (date). For example, if the number of the color combination of red mal e/white female appeared over five observation periods in the order 1, 3, 1, 2, 2, then the minimum number of independent matings required to account for this pattern is 4. This is the minimum estimate of mating frequency because it assumes that the pair observed in the first observation period mated throughout the five periods, and similarly the second pair in the forth period continued through the fifth period. The mean minimum mating frequency of fed females was 1.5 ± 0.96 (SE) and for unfed females was 4.25 ± 0.63 (SE). This difference is significant (t = 2.905, df = 3, $p < .05$).

Effect of feeding on habitat use and mating activity of males

Feeding of males had no significant effect on male habitat use or mating activity. In contrast to females, single males spent the majority of their time on the water surface, and there was no significant effect of feeding treatment on this pattern (refuge use; t = −0.694, df = 3, $p > .5$; Figure 2b). Mean mating activity of males was slightly greater in fed males than in unfed males, but this increase was not significant (t = 1.1, df = 3, $p > .3$; Figure 3). Note that overall mating activity of males and females was not equal because on a few occasions marked males mated with unmarked females that appeared in the pool after the experiment began and were thus not part of our sample.

Resighting efficiency

Our results could be biased by an effect of feeding on resighting rate; however, we did not detect any such bias. Mean resighting rate was high for all classes (fed females = 81.3%, unfed females = 90.8%, fed males = 95.3%, unfed males = 93.3%) and was unaffected by either sex or feeding regime (three-factor ANOVA; date, df = 3, f = 1.67, $p > .2$; sex, df = 1, f = 2.77, $p > .1$; food, df = 1, f = 0.47, $p > .5$; sex × food, df = 1, f = 2.94, $p > .1$). We suspect that most of the non–resighted individuals had left the water surface or were hiding in the near-shore area among the crevices. Addition of these non–resighted individuals to the refuging class would have little effect on the patterns discussed above for male habitat use and would actually strengthens patterns observed for females.

DISCUSSION

Our results demonstrate a tight linkage between condition of female water striders, their habitat choice, and mating dynamics. In the following discussion we focus on the form of this linkage, whether indirect or direct, and its potential consequences. Second, we discuss the lack of effects of condition on male behavior in this experiment and its commonality with prior results. Finally, we draw attention to the primary role that variation in female interests plays in variations in mating dynamics.

Female response

Based on more general treatments of condition-dependent foraging theory (e.g., Ludwig and Rowe, 1990; Mangel and Clark, 1988; McNamara and Houston, 1986), we predicted that fed females would reduce their rate of foraging by retreating to refuge and thereby reduce the associated costs of foraging (predation risk and harassment by males). Single fed females almost doubled their use of refuge; thus, there is a direct link between female condition and habitat choice. Mating activity was reduced dramatically by experimental feeding of females. This may come about through two distinct and potentially complementary mechanisms. First, fed females may mate less simply because their increased use of refuge decreases the rate of harassment by males. In agreement with other studies, we observed that harassment and the commencement of mating occur on the water surface (Krupa et al., 1990; Rubenstein, 1984; Wilcox, 1984). Therefore, there is a direct link between habitat use and mating activity. This set of linkages, direct paths between condition and habitat choice and between habitat choice and mating activity, are shown in Figure 1. Here, the path between condition and mating activity is indirect. This set of paths is supported by our study. In short, hungry females aggregate in habitats where foraging returns are highest. These habitats are also characterized by high levels of harassment from males. Therefore, mating activity of hungry females is increased.

Alternatively, hungry females may be more willing to accept mating to increase their foraging efficiency (Clark, 1988; Rubenstein, 1984; Wilcox, 1984), resulting in a direct path between condition and mating activity (Figure 1). This mechanism could work in concert with the indirect path. We found no support for this hypothesis, but grant that our test was relatively weak. We found that hunger had no effect on the proportion of females using the open-water and near-shore habitats that were mating. A more direct test would be to compare struggle dynamics in fed and unfed females. If there is a direct effect of female hunger on mating activity, we would expect hungry females to struggle less than fed females. Such a test would be extremely difficult to conduct in the wild. However, in a recent laboratory study, Lauer (1995) found no effect of female hunger on the dynamics of premating struggles. In contrast, in this and other water strider species, the response of females to mating attempts (premating struggles) have been shown to vary adaptively with external environment (sex ratio and density) and to explain much of the variation in mating activity (Arnqvist, 1992; Rowe, 1992; Rowe et al., 1994a; Weigensberg and Fairbairn, 1994).

The costs of mating to female water striders include elevated predation risk and perhaps energetic costs of loading (Arnqvist, 1989; Fairbairn, 1993; Rowe, 1994). Both of these costs may be reduced if mating occurs off the water. Mating *Gerris buenoi* use refuge more often than single females (Rowe, 1992). On the other hand, in *A. remigis* (in contrast to *G. buenoi*), one benefit of mating is increased female foraging efficiency. Given these two assumptions we expect that it is in the best interest of females to mate off the water unless foraging needs are high. Our data support this hypothesis. Fed females that were mating spent significantly more time off the water (in refuge) than hungry females that were mating. Nevertheless, a large proportion of mated females in both fed and unfed treatments occurred in refuge (79% and 30%, respectively). Such high proportions are not expected if females accept mates only as means of increasing foraging efficiency. Many of these matings may have occurred simply to reduce costly harassment, and then once started, females fled to the safety of refuge. This behavioral sequence has been documented previously in *G. buenoi* (Rowe, 1992).

The response of *A. remigis* to variation in hunger differed from that reported in a similar study of the lentic water strider, *Gerris buenoi*. Rowe (1992) manipulated the feeding history of both males and females and quantified their mating behavior in the laboratory. Like the current study, short-term feeding history of males had no effect on mating behavior, and feeding history of females significantly affected mating behavior. However, the effect on *G. buenoi* mating activity was opposite to the observed effect on *A. remigis:* mating activity of hungry females was significantly less than that of fed females (Rowe, 1992). Explanations for this difference probably lie in interspecific differences in the relationship between female mating and access to nutrition. In contrast to *A. remigis,* there is no evidence that mating enhances female foraging in *G. buenoi,* but rather it appears to conflict with foraging (Rowe, 1992). Therefore, there appear to be no benefits to females that could balance the known costs of mating (Rowe, 1994).

Male response

In contrast to females, feeding of males had no significant effect on habitat use or mating activity. If the primary value of using risky (open and near-shore) habitats is foraging benefits for males, then we would expect use of these habitats to decrease when males were satiated. However, if the primary benefits of using these habitats is increased access to females, then we would expect little or no difference in habitat use by males in differing hunger states. The latter hypothesis is upheld by the data. The lack of a difference in mating activity between fed and unfed males may be explained solely by a lack of change in habitat use. Matings commence on the water surface, and if average mating activity of males results primarily from their rate of contact with females, then habitat shifts are required to change mating activity. Therefore, our data suggest little effect of hunger on male mating behaviors, such as the rate of mating attempts within habitats or the rate of success in mating attempts.

This lack of an effect of food on male habitat use and mating behavior is consistent with previous studies on water striders (Rowe et al., 1994a). The addition of food to pools had no effect on general activity or mating activity of male *A. remigis* (Sih et al., 1990). Similarly, the removal of food from stream areas had no effect on habitat use by males (Nummelin, 1988). These studies are not directly comparable to the current study because they do not distinguish between the effects of the presence of food and the hunger state of individuals. Previous studies suggest that male feeding requirements are lower than female requirements. Male movement activity is higher than female activity in *Gerris buenoi* (Rowe, 1994), but feeding rates are equal or lower (Rowe, 1992). More female *Limnoporus spp.* responded to offered food than males (Spence and Wilcox, 1986). Similarly, hunger had no effect on mating tactics of male *L. dissortis* (Spence and Wilcox, 1986), or on the mating activity of *G. buenoi* males (Rowe, 1992).

Role of female interests

Previous studies of water striders have focused primarily on how variations in the external environment affect the economics of mating for males and females and on their resulting effects on mating behavior (Arnqvist, in press; Rowe et al., 1994a). A central conclusion of these studies is that much of the variation in mating dynamics and sexual selection can best be understood in terms of adaptive behavioral tactics by females (Arnqvist, 1992; Rowe, 1992; Rowe et al., 1994a). Results of the current study are in agreement with this conclusion. The current study differs from earlier studies in that internal condition rather than external environment was manipulated. However, variation in mating behavior between treatments similarly resulted from variation in female rather than in male behavior.

Summary

Previous studies have led to the general view that ecological conditions drive the evolution of adaptive mating decisions and the diversification of mating systems (Emlen and Oring, 1977; Partridge and Endler, 1987; Rowe et al., 1994a; Vehrencamp and Bradbury, 1984). For example, a variety of environmental conditions have been shown to dramatically affect mating dynamics and sexual selection in water striders (Arnqvist, in press; Rowe et al., 1994a). Here we demonstrated that the nutritional condition of individual females is tightly linked to habitat choice and thereby mating dynamics of water striders in the wild. It is easy to see that in those cases where mating is spatially or temporally associated with foraging (Bradbury et al., 1986; Parker, 1978; Vehrencamp and Bradbury, 1984; Westcott, 1994), variation in the nutritional condition of females may lead to variance in mating behaviors. Our results also add to a growing body of evidence demonstrating that the economic interests of females play a central role in determining mating dynamics (Birkhead and Moller, 1993; Gowaty, 1994; Rosenqvist and Berglund, 1992; Rowe, 1992).

We are grateful to D. Fairbairn, M. Gross, M. Mangel, T. Price, J. Richardson, J. Spence, and D. Westcott for discussion and comments on an earlier draft. This study was funded by U.S. National Science Foundation (NSF) grants BSR 90-20870 and IBN 92-21697 to A.S. and J.J.K., an NSF grant to A.S. and others at the Center for Evolutionary Ecology at University of Kentucky, and a Natural Sciences and Engineering Research Council of Canada postdoctoral fellowship to L.R.

REFERENCES

Arnqvist G, 1989. Multiple mating in a water strider: mutual benefits or intersexual conflict? Anim Behav 38:749–756.
Arnqvist G, 1992. Pre-copulatory fighting in a water strider: inter-sexual conflict or mate assessment? Anim Behav 43:559–567.
Arnqvist G, in press. The evolution of water strider mating systems: causes and consequences of intersexual conflicts of interest. In: So-

cial competition and cooperation in insects and arachnids, vol 1. Evolution of mating systems (Choe JC, Crespi BJ, eds). Princeton, New Jersey: Princeton University Press.

Birkhead T, Moller A, 1993. Female control of paternity. Trends Ecol Evol 8:100–104.

Bradbury JW, Gibson RM, Tsai IM, 1986. Hotspots and the dispersion of leks. Anim Behav 34:1694–1709.

Clark SJ, 1988. The effects of operational sex ratio and food deprivation on copulation duration in the water strider (*Gerris remigis* Say). Behav Ecol Sociobiol 23:317–322.

Crowley PH, Travers SE, Linton MC, Cohn SL, Sih A, Sargent RC, 1991. Mate density, predation risk, and the seasonal sequence of mate choices: a dynamic game. Am Nat 137:567–596.

Dill LM, Fraser AHG, 1984. Riisk of predation and the feeding behavior of juvenile coho salmon (*Oncorhynchus kisutch*). Behav Ecol Sociobiol 16:65–71.

Emlen ST, Oring LW, 1977. Ecology, sexual selection and the evolution of mating systems. Science 197:215–223.

Fairbairn DJ, 1993. Costs of loading associated with mate-carrying in the waterstrider *Aquarius remigis*. Behav Ecol 4:224–231.

Godin J-GJ, Smith SA. 1988. A fitness cost of foraging in the guppy. Nature 333:69–71.

Gowaty PA, 1994. Architects of sperm competition. Trends Ecol Evol 9:160–162.

Gwynne DT, Simmons LW, 1990. Experimental reversal of courtship roles in an insect. Nature 346:172–174.

Houston AI, McNamara JM, Hutchinson JMC, 1993. General results concerning the trade-off between gaining energy and avoiding predation. Phil Trans R Soc Lond B 341:375–397.

Jamieson GS, Scudder GGE, 1977. Food consumption in Gerris (Hemiptera). Oecologia 30:23–41.

Krupa JJ, Leopold WR, Sih A, 1990. Avoidance of male giant water striders by females. Behaviour 115:247–253.

Lauer MJ, 1995. Effect of sperm depletion and starvation on female mating behavior in the water strider *Aquarius remigis*. Behav Ecol Sociobiol (in press).

Ludwig D, Rowe L, 1990. Life history strategies for energy gain and predator avoidance under time constraints. Am Nat 135:686–707.

Mangel M, Clark CW, 1986. Towards a unified foraging theory. Ecology 67:1127–1138.

Mangel M, Clark CW, 1988. Dynamic modelling in behavioral ecology. Princeton, New Jersey: Princeton University Press.

Mangel M, Ludwig D, 1992. Definition and evaluation of the fitness of behavioral and developmental programs. Annu Rev Ecol Syst 23: 507–536.

McNamara JM, Houston AI, 1986. The common currency for behavioral decisions. Am Nat 127:358–378.

Milinski M, Heller R, 1978. Influence of a predator on the optimal foraging behavior of sticklebacks (*Gasterosteous aculeatus* J.). Nature 275:642–644.

Nummelin M, 1988. The territorial behavior of four Ugandan water strider species (Heteroptera, Gerridae): a comparative study. Ann Entomol Fenn 54:121–134.

Nur N, Hasson O, 1988. Phenotypic plasticity and the handicap principle. J Theor Biol 110:275–295.

Parker GA, 1978. Searching for mates. In: Behavioural ecology: an evolutionary approach (Krebs JR, Davies NB, eds). Oxford: Blackwell; 214–244.

Partridge L, Endler JA, 1987. Life history constraints on sexual selection. In: Sexual selection: testing the ideas (Bradbury JW, Andersson MB, eds). New York: John Wiley; 265–277.

Pettersson L, Brönmark C, 1993. Trading off safety against food: state dependent habitat choice and foraging in a crucian carp. Oecologia 95:353–357.

Price T, Kirkpatrick M, Arnold S 1988. Directional selection and the evolution of breeding date in birds. Science 240:798–799.

Price T, Liou L. 1989. Selection on clutch size in birds. Am Nat 134: 950–959.

Rosenqvist G, Berglund A, 1992. Is female sexual behavior a neglected topic? Trends Ecol Evol 6:174.

Rowe L, 1992. Convenience polyandry in a water strider: foraging conflicts and female control of copulation frequency and guarding duration. Anim Behav 44:189–202.

Rowe L, 1994. The costs of mating and female mate choice in water striders. Anim Behav 48:1049–1056.

Rowe L, Arnqvist G, Sih A, Krupa JJ, 1994a. Sexual conflict and the evolutionary ecology of mating patterns: water striders as a model system. Trends Ecol Evol 9:289–293.

Rowe L, Ludwig D, 1991. Size and timing of metamorphosis in complex life cycles: time constraints and variation. Ecology 72:413–427.

Rowe L, Ludwig D, Schluter, D. 1994b. Time, condition and the seasonal decline of avian clutch size. Am Nat 143:698–722.

Rubenstein DJ, 1984. Resource aquisition and alternative mating strategies in water striders. Am Zool 24:345–353.

Sih A, Krupa JJ, Travers S, 1990. An experimental study on the effects of predation risk and feeding regime on the mating behavior of the water strider *Gerris remigis*. Am Nat 135:284–290.

Spence JR, Andersen NM, 1994. Biology of water stiders: interactions between systematics and ecology. Annu Rev Entomol 39:101–128.

Spence JR, Wilcox RS, 1986. The mating system of two hybridizing species of water striders (Gerridae). II. Alternative tactics of males and females. Behav Ecol Sociobiol 19:87–95.

Thornhill R, 1976. Sexual selection and paternal investment in insects. Am Nat 110:153–163.

Vehrencamp SL, Bradbury JW, 1984. Mating systems and ecology. In: Behavioural ecology: an evolutionary approach (Krebs JR, Davies NB, eds). Oxford; Blackwell; 251–278.

Weigensberg I, Fairbairn DL, 1994. Conflicts of interests between the sexes: a study of mating interactions in a semiaquatic bug. Anim Behav 48:893–901.

Westcott DA, 1994. Leks of leks: a role for hotspots in lek evolution? Proc R Soc Lond B 258:281–286.

Wilcox RS, 1984. Male copulatory guarding enhances female foraging in a water strider. Behav Ecol Sociobiol 15:171–174.