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**Daily Patterns of Oviposition Mediate Sexual Conflict
in a Polygynandrous Mating System**

Gina Gentile

A Thesis

in

The Department

of

Biology

Presented in Partial Fulfillment of the Requirements

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ABSTRACT

Daily Patterns of Oviposition Mediate Sexual Conflict in a Polygynandrous Mating System

Gina Gentile

Conflicts of interest between the sexes are considered strong forces in shaping mating systems. Thus an understanding of the behaviour of both sexes is essential. The waterstrider *Aquarius remigis* has been used in several studies investigating sexual conflict. However, little is known about oviposition behaviour or how it affects male / female interactions. In this study, I observed and quantified oviposition behaviour, tested whether the absence of males affected the temporal pattern of oviposition, and looked for relationships between oviposition behaviour and male / female interactions. Females oviposited under water in a manner not previously described for waterstriders. A daily rhythm in oviposition occurred in the absence of temperature cues. Oviposition rates were below average in the early morning, peaked in the evening just prior to 'lights out' or dusk and continued above average for the first few hours of darkness. The absence of males affected the temporal pattern of oviposition, but not the overall daily rate of oviposition. In the absence of males, oviposition rates were above average in the early morning, increased slightly at dusk, and were below average during darkness. Delayed oviposition in the presence of males was not due to prolonged copulation since females initiated oviposition around the same time regardless of their copulation history. Females were much more reluctant to mate before oviposition than after oviposition. The daily rhythm of oviposition and the effect of oviposition on female reluctance alter the intensity of

sexual conflict and sexual selection over the course of the day.

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Introduction

Conflicts of interest between the sexes (sexual conflict) often arise because males and females attain reproductive success by different means (Trivers 1972; Parker 1979; Dawkins 1989). Males attain greater reproductive success primarily by increasing the number of eggs they fertilize, while females attain greater reproductive success primarily by increasing the quantity and/or quality of eggs they produce (Bateman 1948; Trivers 1972). This hypothesis predicts that males should invest most of their time and energy pursuing copulation with as many females as possible, while females should invest primarily in seeking high quality mates, resources for the production of eggs, and safe environments for their young (Bateman 1948; Trivers 1972; Bailey and Ridsdill-Smith 1991; Andersson 1994). Sexual interaction between males and females can be considered obligate mutualism because some compromise in behaviour must occur (Alexander et. al. 1997). For example, females may mate longer or more often than is required to maximize fertility (e.g. Carroll 1991; Schulze-Hagen et. al. 1995; Dickinson 1997), and males may spend time and energy searching for or defending resources attractive to females rather than searching for additional mates (e.g. Thornhill 1983).

Examining mating systems in terms of sexual conflict is relatively new. The majority of past studies focused primarily on male behaviour and consequently failed to recognize that the reproductive interests of males and females often differ (issue discussed in: Eberhard 1990, 1996; Gowaty 1994; Fincke et. al. 1997). Sexual conflict is now considered a strong selective force in shaping mating systems (Parker 1979; Arnqvist and

Rowe 1995; Clutton-Brock and Parker 1995; Chapman and Partridge 1996; Alexander et. al. 1997; Arnqvist 1997; Stockley 1997), and therefore, the reproductive behaviour of both sexes must be studied (Birkhead and Møller 1993a; Gross 1994; Stockley 1997). Because female reproductive interests were often neglected in the past they have been the focus of a large body of current research.

A female's behavioural response to the opposite sex often changes with her egg maturation cycle (Stacey 1981; Thornhill and Alcock 1983; Fincke 1988; Montgomerie and Thornhill 1989; Arvidsson 1992). At one point in the cycle a female may not accept any copulation attempts while at another she may incite males to compete with each other for access to copulate (e.g. Cox and Le Boeuf 1977; Callahan 1981; Montgomerie and Thornhill 1989; Poole 1989). Because insemination and fertilization are often temporally separated (Birkhead and Møller 1993a & 1993b; Alexander et. al. 1997; Stockley 1997), a female may control paternity of her offspring by mating with additional males before fertilization occurs (Hill et. al. 1994; O'Connell and Cowlshaw 1994; Kempnaers et. al. 1995; Siva-Jothy and Hooper 1996; Eberhard 1997). Within the female's reproductive tract the sperm from the different males must compete to fertilize the eggs (Sperm Competition: Parker 1970; reviewed by Birkhead and Hunter 1990). However, a male's sperm will have a fertilization advantage over the sperm of rivals if deposited at the right time in the female's egg maturation cycle. For example, in females that can store sperm (as in some mammals, reptiles, birds, and many insects; Birkhead and Møller 1993b) a last male mating advantage is common. Males have evolved several behavioural tactics to gain

access to females during this time, and others to prevent rivals from taking their fertilization advantage away once obtained (Parker 1970; Alcock et. al. 1977; Alcock 1994; Andersson 1994).

Mate guarding is one tactic by which males may gain a fertilization advantage over other males (Parker 1970). By guarding, a male may prevent the female from acquiring sperm from rival males before egg fertilization occurs (e.g. Ward 1986; Sherman 1989; Arvidsson 1992; Frankino and Sakaluk 1994; Storey et. al. 1995). In some groups, males guard their mates by remaining *in copula* (genitals engaged) longer than is required for successful sperm transfer (e.g. Sillén-Tullberg 1981; Rubenstein 1989; Cordero 1990; Carroll 1991; Michiels 1992). In these prolonged copulations the male is, in a sense, using his genitalia as a plug to prevent other males from inseminating his mate.

Frequent copulation is also viewed as a male tactic to ensure fertilization (e.g. Schulze-Hagen et. al. 1995). By mating with several females, or repeatedly with one female, a male increases the probability of higher reproductive success (e.g. Oglesby et. al. 1981; Møller and Birkhead 1993). Female reproductive success however, may not increase with either prolonged or frequent copulation (Thornhill and Alcock 1983; Arnqvist 1997). Long copulations may prevent females from foraging, reduce their mobility, and in some cases make them more susceptible to predation (Fairbairn 1993; Stockley 1997). Frequent copulation may be energetically costly and unnecessary in terms of sperm requirements (Arnqvist 1989; Fairbairn 1993). Females of insect species that can store sperm, for example, commonly require only one to a few inseminations to fertilize

every egg in their lifetime (Ridley 1988). It is clear that a conflict of interest exists between the sexes over copulation duration and frequency.

The stream-dwelling waterstrider, *Aquarius remigis* (Hemiptera: Gerridae) has been used in several studies investigating sexual conflict (Rubenstein 1989; Krupa and Sih 1993; Weigensberg and Fairbairn 1994, 1996; Sih and Krupa 1995; Lauer et. al. 1996). *Aquarius remigis* has a polygynandrous mating system, both males and females mate many times with different individuals during a two to three month reproductive season from early spring to early summer (Fairbairn 1985; Krupa and Sih 1993; Sih and Krupa 1995; Preziosi and Fairbairn 1996). Males actively search for, and attempt to mate with females as they are encountered on the stream (Scramble Competition Polygyny: Thornhill and Alcock 1983; Arnqvist 1997). Females generally respond to harassing males with resistance (about 85 % of the time; Weigensberg and Fairbairn 1994). In these cases a pre-copulatory struggle ensues and females are often successful in preventing males from mounting (about 57 % of the time; Weigensberg and Fairbairn 1994). Female reluctance to superfluous mating has been attributed to the female's need to mate only once every 15 days to maintain full fertility and fecundity (Fairbairn unpublished; Weigensberg and Fairbairn 1996).

The intensity of female reluctance to mate has been found to depend on male density (Krupa and Sih 1993; Sih and Krupa 1995). When male density is high, females experience higher encounter rates with harassing males. Mating females however, are harassed less often than solitary females (Wilcox 1984). Thus, when harassment reaches

high levels a female becomes less reluctant to mate (Krupa and Sih 1993; Lauer et. al. 1996). At this point the cost of repelling males has exceeded the cost of mating. Therefore, females mate out of convenience to avoid harassment from solitary males (Convenience Polyandry: Thornhill and Alcock 1983; Arnqvist 1997).

Copulations are variable in duration ranging from less than one hour to more than 12 hours (Wilcox 1984; Fairbairn 1988a; Weigensberg and Fairbairn 1994). Insemination however, is believed to occur between 15 to 30 minutes after genital contact (Rubenstein 1989). Females can store sperm, eggs are fertilized as they are laid, and the last male to mate before oviposition fertilizes on average 65 % of the eggs (Rubenstein 1989). The prolongation of copulation is considered a male mate guarding tactic (Clark 1988).

Prolonged copulations may only be advantageous for females when male harassment levels are high. If a female is ready to oviposit but is unsuccessful in dislodging a mate she must postpone oviposition. Most prolonged copulations are terminated by a post-copulatory struggle (81%; Weigensberg and Fairbairn 1994). A conflict of interest over copulation frequency and duration clearly exists in this species.

Despite this information on sexual conflict in *A. remigis*, the relationship between the female's egg maturation cycle and mating behaviour has not been fully investigated. Little is known about female egg laying (oviposition) behaviour, and what is known is based on anecdotal evidence (Matthey 1975). Females have been observed to oviposit more or less on a daily basis, but it is not known whether they oviposit at a particular time of day. Daily rhythms in oviposition are common in insects (e.g. Crawford 1967; Loher and

Chandrashekar 1970; Rankin et. al. 1972; Skopik and Takeda 1980; Shaerer et al. 1995; Tessmer et. al. 1995) and could cause significant daily patterns in mating behaviour. A daily rhythm in oviposition could alter both the intensity of sexual selection and sexual conflict over the occurrence and duration of copulations at different times of the day. For example, we would expect the intensity of sexual selection to be most intense just prior to oviposition because the last male to inseminate the female will fertilize the majority of her eggs (Rubenstein 1989). Female reluctance should also increase just prior to oviposition because females only oviposit when solitary. To oviposit females must therefore terminate copulations in progress and repel subsequent copulation attempts. This increase in both the fitness pay-offs for males and female reluctance to mate just prior to oviposition produces a clear conflict of interest between the sexes over copulation at this time.

Given the pre-existing literature on sexual conflict and the mating system in *A. remigis*, and the lack of information about female oviposition behaviour, the objectives of my thesis are 1) to describe and quantify oviposition behaviour, 2) to determine whether there is a daily rhythm to oviposition, and 3) to look for relationships between oviposition behaviour and male / female interactions.

Methods

Aquarius remigis is a large semi-aquatic bug (11 - 15 mm) which inhabits streams and small rivers throughout North America. The majority of Canadian populations are univoltine (Galbraith and Fernando 1977; Fairbairn 1985). Adults diapause during the winter and emerge reproductively active in the spring (Galbraith and Fernando 1977; Fairbairn 1985).

Preliminary Experiment To design experiments suitable for my thesis objectives I first required some knowledge of the temporal pattern of oviposition in *A. remigis*. I also needed to determine whether feeding time affected the temporal pattern of oviposition. Waterstriders were collected from the south creek of the McGill field station at Mont St. Hilaire on September 20, 1995 and placed in the laboratory refrigerator at 2 °C to diapause on the same day. On February 12, 1996, 25 male and 25 female waterstriders were removed from diapause and placed in a stream tank (140 x 50 x 25 cm), similar in design to those used by Fairbairn and Brassard (1988), in the laboratory where a 16L : 8D light cycle was maintained. Frozen fifth instar (length = 1.2 cm) crickets (*Acheta domesticus*) were provided for food in excess of the waterstrider's daily energy requirements.

One week later, one male and one female were placed in each of 20 cages (40 x 27 x 14 cm) in an incubator at 22 °C, and 16L : 8D. Each cage contained an air stone to create surface water movement, an upside down polystyrene cup (height = 8.5 cm) weighed down with a stone for resting and oviposition, and water to a depth of approximately 5

cm. I provided each pair with 12 frozen adult fruit flies (*Drosophila melanogaster*) per day. Although quantities should have been sufficient for maximal fecundity (Blanckenhorn et. al. 1995) after six days the females were laying few, if any eggs. The fruit flies may have been desiccated and I suspected that the females were not getting the necessary nutrients to produce eggs. On that day I switched back to feeding each pair one cricket per day. This quantity of food was more than sufficient to maintain full fecundity (Ferguson unpublished; Blanckenhorn et. al. 1995). The experiment was initiated three days later. Eggs were counted and removed from the polystyrene cups at 0600, 1000, 1400, 1800, and 2200 for six days. Waterstriders were fed at 0900 for the first three days and then at 1800 for the last three days.

The egg counts for each time interval were averaged over days for each female for each feeding treatment. The mean values were then converted into number of eggs laid per 2 h. Converting into rates was necessary for making comparisons between time intervals of different duration. For example, the overnight time interval was 8 h while the others were 4 h. The rates of oviposition for the first three days of the experiment were much less variable than those for the last three days. This was most likely an effect of the feeding of fruit flies before the start of the experiment. It can take up to a week for females to start laying normal numbers of eggs after being starved (Ferguson unpublished). Therefore, females were laying fewer eggs than normal during the first three days of the experiment but had recovered by the last three days of the experiment. To use these data in an ANOVA without violating the assumption of homoscedasticity, I

standardized the rates of oviposition to a daily mean of zero and standard deviation of one.

Focal Observations To describe and quantify daily patterns in oviposition and look for relationships with male / female interactions, focal females were videotaped continuously with a high resolution camcorder (Sony CCDTRV70) in the laboratory. Waterstriders for the first set of observations were collected on June 9, 1996 near Morin Heights, Quebec and were used for 20 days of recording between June 11 and July 11, 1996. Waterstriders for a second set of observations were collected near Mont-Tremblant, Quebec on September 14, 1996 and placed in a refrigerator to diapause from September 20, 1996 until February 26, 1997. They were used for 15 recording days between March 10 and April 1, 1997. All waterstriders were placed in stream tanks to acclimate to laboratory conditions before the start of observations, and individuals not being used for recording were kept in these stream tanks. Frozen crickets (*A. domesticus*) were added to the tanks each day at approximately 1200. All waterstriders, whether being recorded or not, experienced the same light cycle (16L : 8D), ambient air temperatures (21 - 25 °C), sex ratio (1:1), and quantity of food (one cricket per two waterstriders per day).

The experimental apparatus consisted of a glass aquarium (44 x 24 x 30 cm) containing approximately 8 cm of water, an air stone, and a piece of polystyrene sealed to the center of one of the long sides (Figure 1). The polystyrene sloped down into the water and rested on the bottom of the aquarium. Half of the polystyrene was above the surface of the water and half was below. This served the dual purpose of a resting site above the

Figure 1

Experimental apparatus used for the focal observation. The view is similar to that recorded by the camcorder. A: resting / oviposition site; B: waterstrider; and C: mirror. Note the horizontal view reflected in the mirror which shows both above and below the water surface.



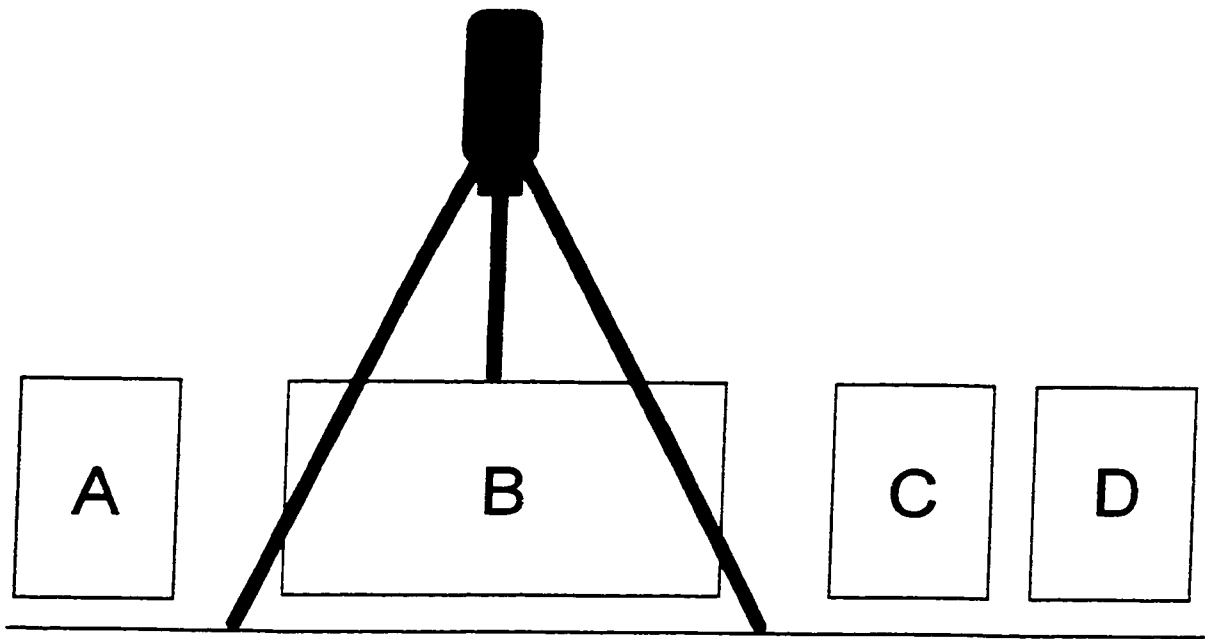
surface of the water and a substrate for oviposition below the surface of the water. The camcorder was mounted vertically above the aquarium, and a mirror was placed at a 45 ° angle on the opposite side of the aquarium from the polystyrene resting/oviposition site to reflect a horizontal view of the water surface (Figure 1). This setup allowed me to identify individuals and observe mating interactions from above, and at the same time, observe the intricacies of oviposition behaviour from the side. All remaining sides of the aquarium including the bottom were covered with white paper to increase the contrast between the waterstriders and the background and to prevent the waterstriders from being disturbed.

Each trial consisted of 12 h of continuous recording beginning at 1000 and ending at 2200. Recording began at 1000 rather than when the lights turned on (0600) because the preliminary experiment indicated that little mating or oviposition occurred during this time interval. At approximately 2200 the night before each trial two new females and two new males were selected haphazardly from the stream tanks. To differentiate individuals in a given trial, one female and both males were marked with yellow nontoxic enamel paint. The marked female was then placed in the 'recording' aquarium with one male (Figure 2, tank B), and the unmarked female and remaining male were placed in an adjacent aquarium of the same dimensions (Figure 2, tank A). The unmarked female and remaining male were transferred into the 'recording' aquarium just before the start of the trial. At the end of every trial, eggs on the oviposition site were counted and removed. Females were unable to lay eggs on the smooth walls of the aquarium. Eggs deposited the night before the trial (2200 - 1000) were counted and during the second set of observations; I

Figure 2

A diagram of the aquaria used for quantifying oviposition during focal observations.

Aquaria A, C, and D are sideways to the recording aquarium B. At 2200 the night before the trial an unmarked female and one male were placed in aquarium A and a marked female and one male were placed in aquarium B. Just before 1000 the following day the waterstriders were removed and the oviposition sites checked for eggs. These four individuals were then placed in aquarium B and the video trial began at 1000. After the trial (2200) the marked female and one male were placed in aquarium C and the unmarked female and one male were placed in aquarium D. The oviposition site in aquarium B was checked for eggs. At 1000 the following day waterstriders were removed from aquaria C and D and the oviposition sites were checked for eggs.



also counted eggs laid the night following the trial (2200 - 1000) (Figure 2).

From the video tapes I recorded the start and finish times of ovipositions, copulations, pre-copulatory struggles, and post-copulatory struggles. Start and finish times of struggles that did not result in copulation were also recorded for the first set of observations. Durations and frequencies were then calculated for these behaviour patterns. I will refer to copulations in which sperm were most likely transferred as 'long' (greater than or equal to 15 minutes) and those in which sperm were not likely transferred as 'short' (less than 15 minutes; Rubenstein 1989). Latency is defined as the duration of time between termination of the last copulation before oviposition and initiation of oviposition. Females are categorized by the last copulation that they experienced before oviposition: 1) long, 2) short, 3) none. Only one female from each trial was used to maintain independence of data. I alternately selected marked and unmarked females from trials in which both females could be used.

Field Scan Sampling To observe and quantify the oviposition behaviour of *A. remigis* in its natural habitat, scan sampling was performed for eight days at the south creek of the McGill field station, Mont St. Hilaire, Quebec between May 28 and June 9, 1996. Plastic wading pools (diameter = 1.22 m) were placed in the creek, filled with approximately 5 cm of water. In each pool, three partially submerged rocks served as ballast and places for the waterstriders to rest and oviposit. For the first four days, seven pools were used. Three more pools were added for the last four days for a total of ten pools.

Each pool contained five males and five females collected from the south creek

immediately before use. The males in each pool were marked on the thorax with numbers from one through five with nontoxic yellow enamel paint. The females were marked on their mid- and hind- femora so that identification could be possible while they mated. Frozen crickets (*A. domesticus*) were provided as food in excess of daily requirements.

The first four days of the experiment were consecutive and used the same individuals in each pool. Overnight rain storms during the last four days facilitated the escape of individuals. As a consequence, all waterstriders were replaced in the pools before the fifth day of the experiment, once again before the sixth day, and one last time before the eighth day. To ensure independence, the within pool data were averaged over days for pools which used the same individuals (days 1 - 4, and 6 - 7). This yielded 37 independent data points (waterstrider groups) for analysis.

The behaviour of each female was recorded every 30 min from 0600 until we could no longer see at 2130. Each scan took approximately 5 min. The categories of behaviour recorded were 1) on or off the water, 2) solitary, mating, ovipositing, or not seen. Ambient air temperature, and water temperature in the pools were also recorded each scan. Rocks were inspected for eggs every 2 h starting at 0600 and ending at 2000. Eggs were counted and removed, and the rocks scrubbed before being replaced in the pools.

Oviposition was quantified using both frequency of observation and egg counts. For observed oviposition, the scanning day (0600 - 2130) was divided up into four time intervals (all 4 h except the last which was 3.5) and the number of waterstrider groups in which oviposition was observed each time interval was tabulated. Egg counts were

pooled into four 4 h time intervals between 0600 and 2000 plus overnight (2000 - 0600). Oviposition rates (number of eggs laid per 2 h) were calculated for each time interval for each waterstrider group. The rates were then standardized within waterstrider groups by subtracting their mean daily oviposition rate.

Laboratory Scan Sampling Experiment The purpose of this experiment was to examine the daily rhythm of oviposition in the absence of temperature cues, and determine whether the daily rhythm was affected by the presence of males. In the laboratory, daily patterns of oviposition were quantified for groups of females in one of two treatments: 1) males absent, or 2) males present (1:1 sex ratio). The waterstriders used were from the sample collected near Mont-Tremblant for the focal observations.

The experimental apparatus consisted of six stream tanks filled with water to a depth of approximately 10 cm. Fifteen upside down polystyrene cups (height = 8.5 cm) each weighed down with a rock were placed in each of the stream tanks to serve as resting and oviposition sites. Light cycle, ambient air temperature, and food quantity were the same as for the focal observations.

On February 26, 1997 individuals were selected haphazardly from containers in which they had diapaused and then distributed among the tanks until each contained 15 females and seven or eight males. These groups were maintained for ten days to ensure that all females were inseminated before the start of the experiment. The two treatments were initiated by first removing the males from the stream tanks and then placing 15 males back into each of three of the tanks. Three tanks thus had only 15 females, and three tanks had

15 females and 15 males. Because mating frequency tends to be lower in established pairs (Preziosi unpublished) all males were placed with females new to them. Treatments (presence or absence of males) were alternated among the six tanks.

Beginning on March 10, eggs were counted and removed from oviposition sites every 4 h between 0600 and 2200, with an additional count at 2400. After five days, the treatments were reversed: males were removed from the tanks which had a 1:1 sex ratio, and added to the female only tanks. After one day for acclimation, the experiment resumed and eggs were counted for another five days. Data from each waterstrider group (tank) were standardized as follows. Oviposition rates (number of eggs laid per two hours) were calculated from egg counts for six time intervals. The six rates for each day were then standardized by subtracting that day's mean oviposition rate for all tanks combined. The standardized oviposition rates at each time interval were then averaged over days for each treatment. Each waterstrider group thus had two standardized oviposition rates for each of the six time intervals, one from the males present treatment and one from the males absent treatment. The standardization removed differences among days but not among treatments.

Statistical Methods Repeated measures ANOVA was used when a variable was measured more than once for each individual. For example, rates of oviposition were measured at different times for the same individual. Using the method proposed by Girden (1992), violations of the assumption of sphericity were dealt with as follows. If the coefficient of sphericity ' ϵ ' was less than 1 but greater than 0.75, a multivariate repeated

measures ANOVA was used unless the number of within group treatment levels exceeded the number of groups. In this case a univariate model was used with a Huynh-Feldt ' ϵ ' correction to the degrees of freedom. If ' ϵ ' was less than 0.75, a multivariate model was used unless the number of within group treatment levels exceeded the number of groups. In this case a univariate model was used with a Greenhouse-Geisser ' ϵ ' correction to the ' df '. The three multivariate repeated measures ANOVA test statistics (Wilks, Pillais, and Hotellings) all yielded the same F-values and probabilities. Therefore, I have not specified which test was used. All t-tests are two-tailed.

Results

1) Oviposition Behaviour of Female *A. remigis* All females initiated oviposition by walking backwards down the oviposition site. Occasionally they stopped when only their abdomens were under water, but more typically they continued until completely submerged. I observed females right at the bottom of a stream tank about 10 cm below the water surface. During their descent, all females continuously tapped the substrate with their abdomen in a side to side motion. This behaviour terminated when the female leaned back into a position where her ovipositor came in contact with the substrate. She remained in this position while depositing her egg (s). Eggs were always placed lengthwise (lying on their long axis), and commonly within pits and crevices on the substrate. The “leaning-back” position was always associated with oviposition of at least one egg. The female would then either continue the pre-oviposition abdominal tapping or would return to the water surface by crawling up the substrate head first. Each trip down into the water and back out was considered one bout of oviposition.

A question of independence arose upon analysing the data from the focal observations because two females were present in every video trial. Oviposition is likely an independent act, because males do not guard mates while they oviposit and the oviposition site was large enough to accommodate more than one female at time. I have observed up to three females ovipositing at the same time on smaller oviposition sites in the laboratory on several occasions. For this reason basic descriptive statistics of oviposition such as number of bouts, duration of time spent per bout, total duration of time spent per day, and

duration of time spent under water per egg deposited were calculated using all ovipositing females regardless of whether they were in the same trial. Data from the two populations (Morin Heights, and near Mont-Tremblant) were pooled as there were no significant differences between them except in the percentage of females that oviposited. The proportion of ovipositing females, 32.5% and 66.7% respectively, differed significantly ($\chi^2 = 8.03$, df 1, $P < 0.005$). All 10 of the females that did not oviposit during the trial in the second set of observations oviposited within 2 h after recording ended. Oviposition was not monitored the night after the trial in the first set of observations.

The following descriptive statistics (means, standard deviations, and ranges) are based on 33 females that oviposited during their recorded trial (1000 - 2200). On average females had 4.6 ± 3.8 (range, 1 - 15) bouts of oviposition and spent 8.97 ± 10.63 (range, 0.92 - 51.35) min under water per bout. Mean total time spent ovipositing during the 12 h of video recording was 30.65 ± 29.67 (range, 0.92 - 121.68) min. The number of eggs laid per female per trial was based on trials in which only one female laid eggs so that all eggs could be ascribed to a single known female. Mean number of eggs laid during a trial for 13 females was 6.23 ± 2.89 (range, 2 - 10). Mean number of eggs laid over a 24 h period (the night before the trial plus during the trial) for 39 females including those that did not lay any eggs was 6.10 ± 4.14 (range, 0 - 14). The average amount of time spent under water to lay one egg was 5.73 ± 3.44 (range, 1.59 - 11.21) min. This value includes both time spent searching for a site and time spent depositing the egg. Total time spent ovipositing and number of eggs laid were not significantly correlated ($r = 0.389$, df 11, $P =$

0.189).

2) Daily Rhythm in Oviposition A daily rhythm in oviposition was observed. The preliminary experiment indicated that feeding time did not significantly affect the daily rhythm (Multivariate Repeated Measures ANOVA, Time of day x Feeding time interaction, $F = 1.831$, $df 4, 11$, $P = 0.193$). In the field, oviposition was rarely observed in the early morning and most commonly observed in the early evening ($\chi^2 = 14.091$, $df 3$, $P = 0.0028$; Figure 3). This pattern was also found in the standardized rates of oviposition calculated from egg counts in the field (Multivariate Repeated Measures ANOVA, $F = 3.081$, $df 4, 27$, $P = 0.033$; Figure 4). Rates of oviposition were lowest between 0600 and 1000, and greatest between 1400 and 2000.

The daily rhythm of oviposition was similar in the laboratory. Time of day explained a significant amount of the variance in oviposition rate in the preliminary experiment (Multivariate Repeated Measures ANOVA, $F = 90.475$, $df 4, 11$, $P < 0.0005$). As in the field, rates of oviposition were lowest between 0600 and 1000 and highest between 1400 and 2000 (Figure 5). Females from the focal observations started their first bout of oviposition on average at 1717 ± 3 h 7 min. The median time of day between the start of the first bout of oviposition and the end of the last bout of oviposition was on average 1811 ± 2 h 49 min (Figure 6). The laboratory scan sampling experiment also showed the same daily rhythm in oviposition and is described in the following section. Although there was a large variance among females, the majority of females laid eggs during the evening both in the laboratory and field. Air temperature showed a daily pattern in the field

Figure 3

Proportion of waterstrider groups in which at least one oviposition was observed as a function of time of day. Data are based on scan samples of groups of five male and five female *A. remigis* at 30 min intervals between 0600 and 2130, at Mont St. Hilaire, Quebec. Total number of waterstrider groups = 37.

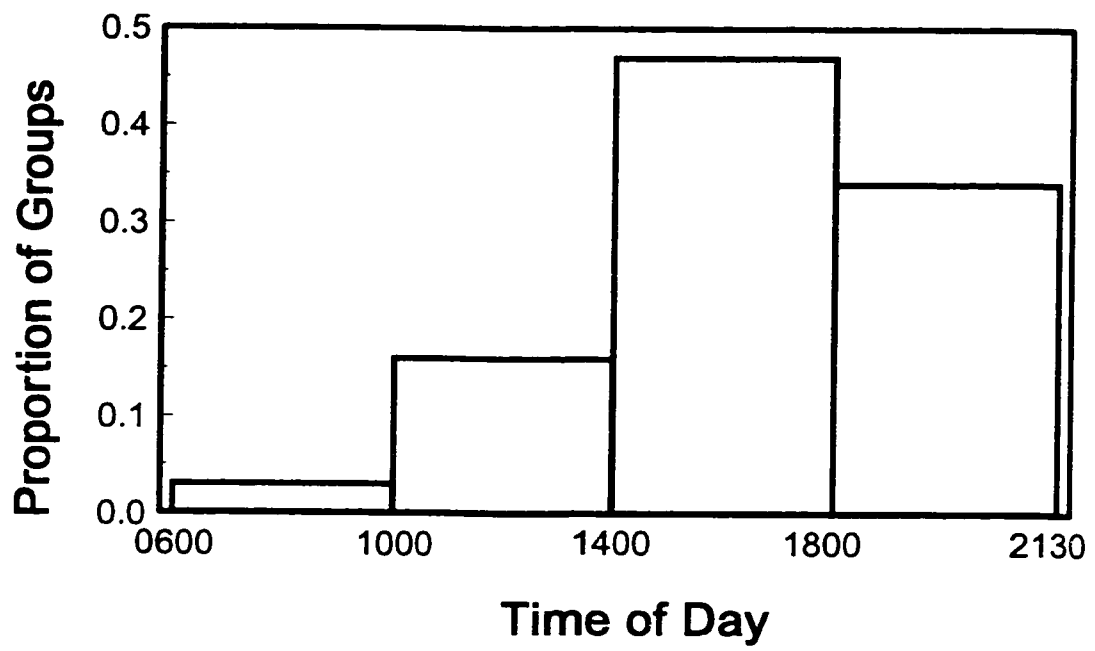


Figure 4

Mean (\pm SE) standardized oviposition rates (number of eggs laid/ 2 h) for five time intervals dividing the 24 hours of the day. Center line represents the mean daily oviposition rate. Rates were calculated from egg counts at two hour intervals between 0600 and 2000 for 37 independent groups of 5 male and 5 female *A. remigis* in the field, at Mont St. Hilaire, Quebec. The egg count at 0600 quantified overnight oviposition. Data for each group are standardized to their own daily means.

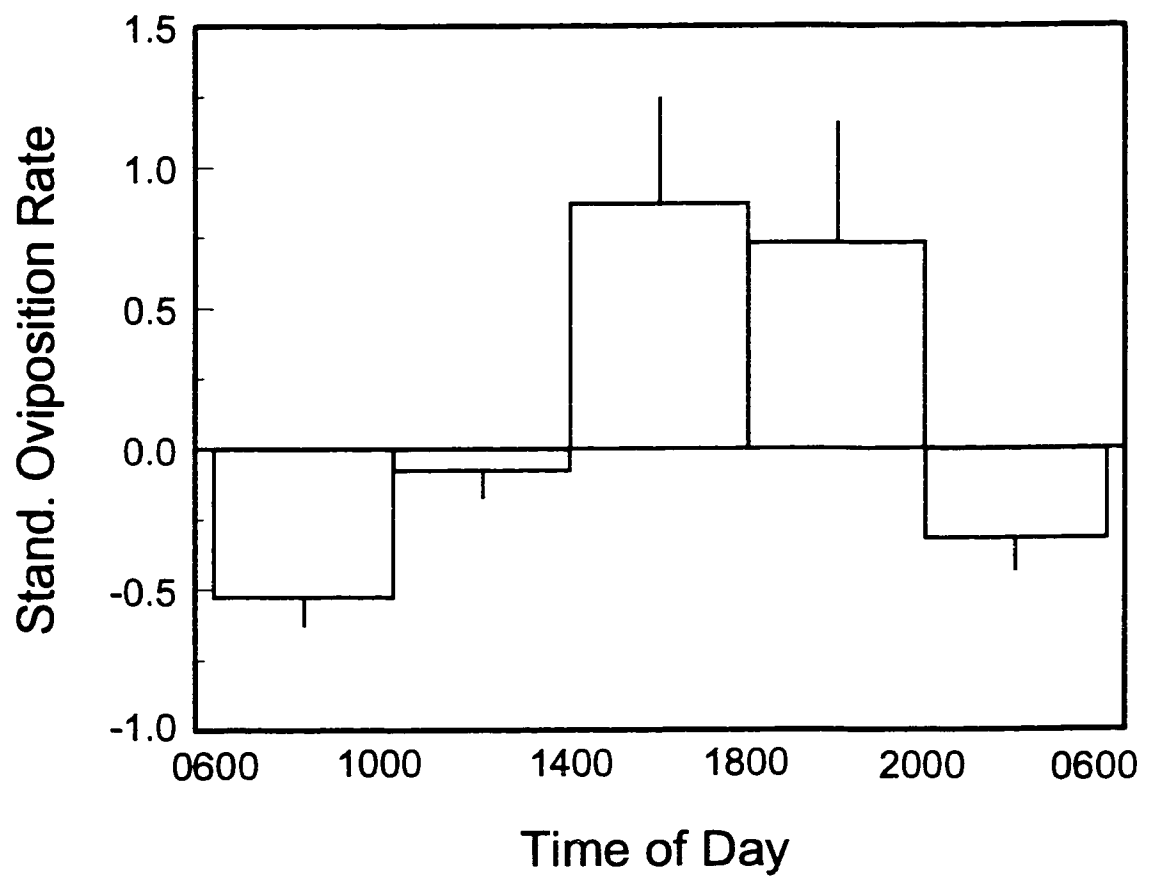


Figure 5

Mean standardized oviposition rates (number of eggs laid/ 2h) for five time intervals dividing the 24 hours of the day. The center line represents the mean daily oviposition rate. Rates were calculated from egg counts at four hour intervals between 0600 and 2200 for 15 pairs (male / female) of *A. remigis* in the preliminary experiment. The egg count at 0600 quantified overnight oviposition. Data for each female have been standardized to their own daily mean and standard deviation.

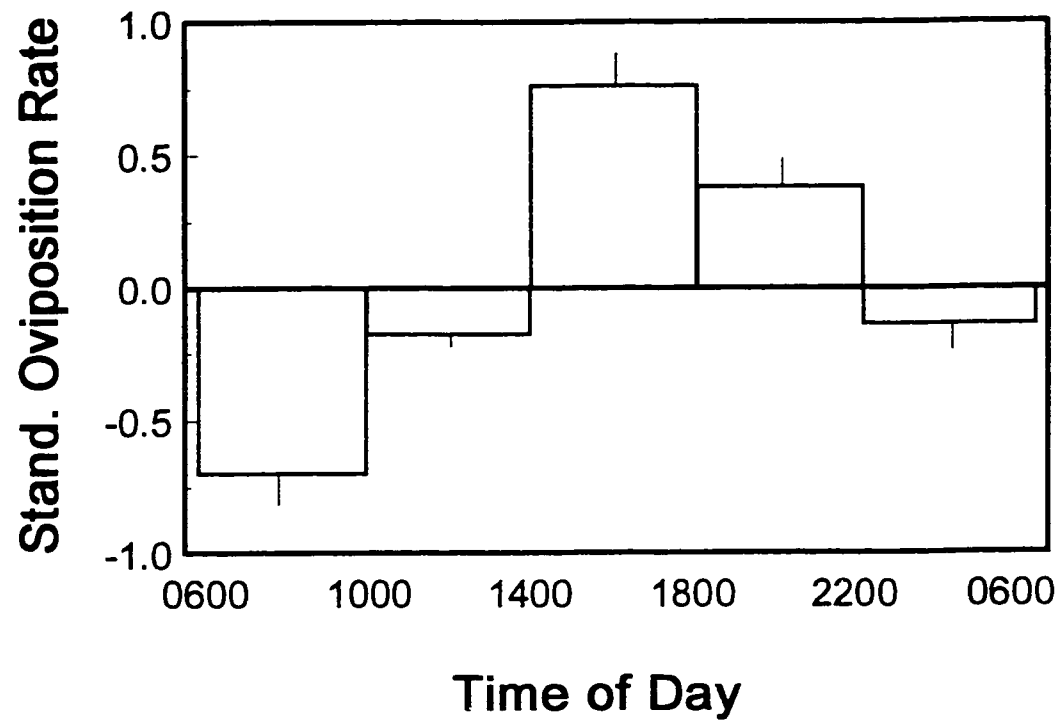
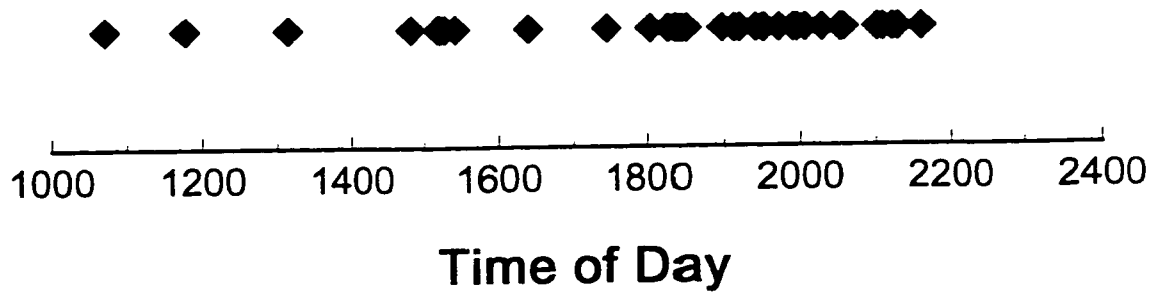


Figure 6

Median times of day at which 33 video-recorded females were ovipositing. Each data point represents one female.



(Figure 7), but this variation was not required for the daily rhythm in oviposition since a similar oviposition rhythm occurred both in the incubator, where temperature was constant, and in the laboratory where temperature showed little daily variance.

3) Relationships Between Oviposition Behaviour and Male / Female Interactions

A univariate repeated measures analysis of variance was used to determine the effect of time of day, males, and order of treatment (males present or absent first) on the daily rhythm of oviposition rates in the laboratory scan sampling experiment. Oviposition rate varied significantly with time of day, but this pattern was strongly influenced by the presence or absence of males (Figure 8, Table 1). The presence of males had no significant effect on the overall daily rate of oviposition, but had a significant effect on the daily rhythm of oviposition rates. In the presence of males, the daily rhythm of oviposition was very similar to that found during field scan sampling, in the preliminary experiment, and focal observations. Oviposition rates were lowest in the early morning and highest in the early evening peaking between 1800 and 2200 (Figure 8 b & c). In the absence of males a significant daily rhythm in oviposition rate was observed, but rates were generally more evenly distributed over the day: oviposition rates were above average in the early morning, increased slightly at dusk, and below average in darkness (Figure 8 a & d). The order in which the treatments were experienced did not have a significant effect on the daily rhythm of oviposition (Table 1).

To see whether a relationship exists between oviposition behaviour and copulation history I compared females that experienced different types of copulations (long, short, or

Figure 7

Daily pattern of air temperature change at the south creek, Mont St. Hilaire, Quebec during scan sampling. Minimum and maximum temperature lines are also illustrated.

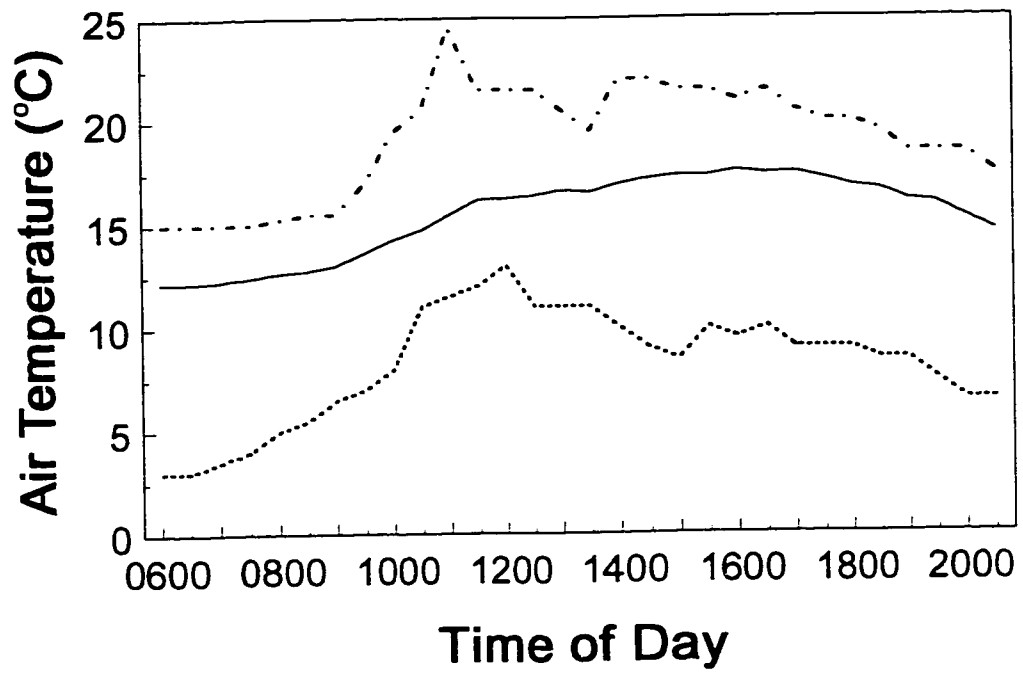


Figure 8

Mean (\pm SE) standardized oviposition rates (number of eggs laid / 2 h) for six time intervals dividing the 24 hours of the day. The center line represents the mean daily oviposition rate. Rates were calculated from egg counts at four-hour intervals between 0600 and 2200 and an additional count at 2400 in the laboratory scan sampling experiment. Data for each group are standardized to the daily mean of all groups combined. Viewing the figures from left to right illustrates the difference between treatments within the same tanks. Viewing the figures from top to bottom illustrates the difference between treatments between different tanks. Dotted line = transition from light to dark.

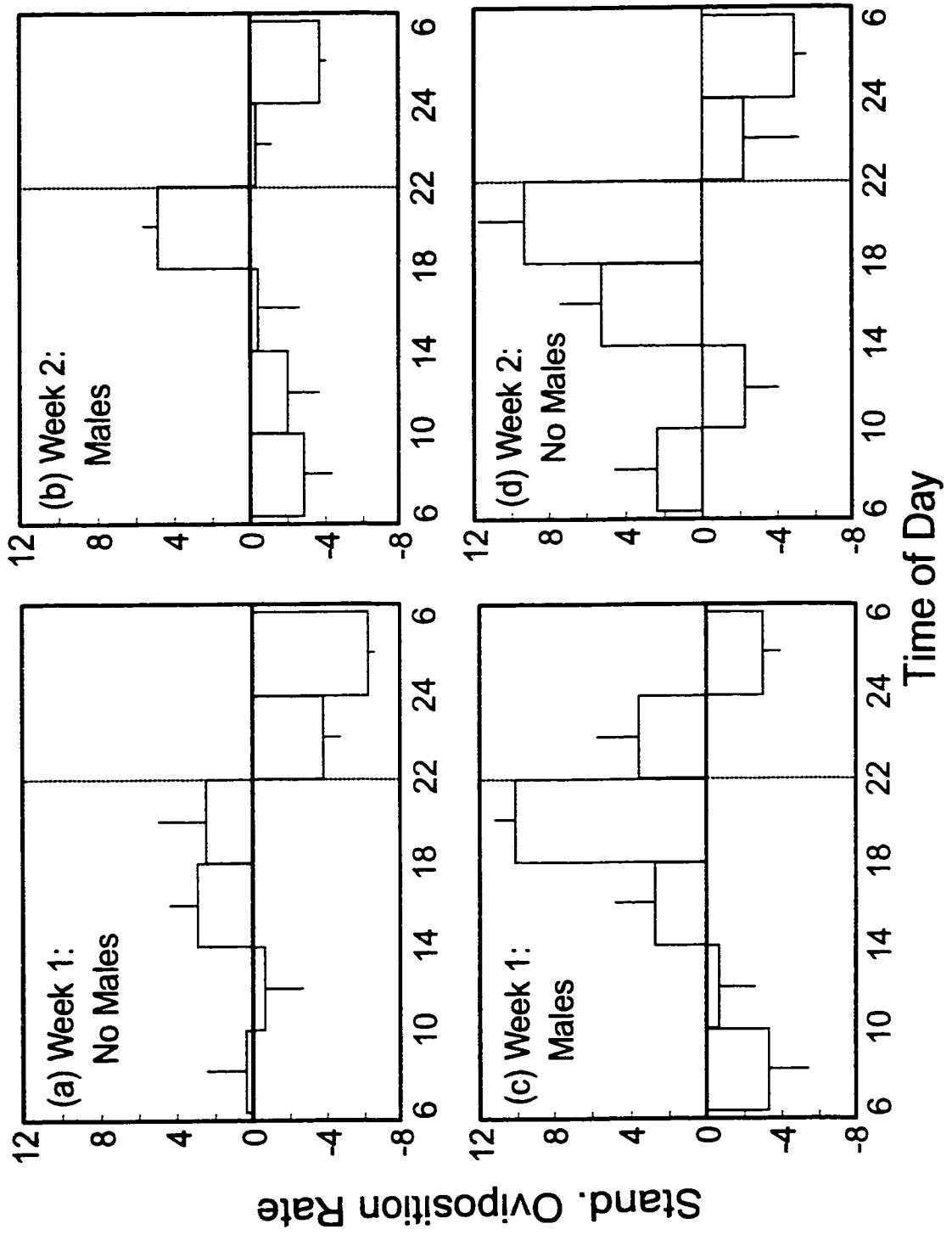


Table 1
 Univariate repeated measures ANOVA results for the effect of time of day, males, and the order of treatment (males present or absent first) on standardized rates of oviposition (number of eggs laid / 2 h). Data collected from the laboratory scan sampling experiment.

Source of Variance	F	df	P
Time of Day	30.941	5, 20	0.000
Males	0.294	1, 4	0.616
Order of Treatment	1.285	1, 4	0.320
Time of Day * Males	9.622	5, 20	0.010
Time of Day * Order of Treatment	2.531	5, 20	0.116
Males * Order of Treatment	0.108	1, 4	0.759
Time of Day * Males * Order of Treatment	0.995	5, 20	0.407

none) preceding oviposition. No significant difference was found in the mean time of day at which long copulations (1421 ± 3 h 40 min) and short copulations (1456 ± 1 h 47 min) began (t-test with unequal variance, $t = 0.43$, $df = 13.65$, $P = 0.676$) (Figure 9). However, the time at which long copulations started was much more variable than that of short copulations (Levenes's test for equality of variance, $F = 5.886$, $df = 3, 11$, $P = 0.029$). Latency to oviposit was much longer for females that had short copulations (2.61 ± 1.50 h) than for those that had long copulations (0.61 ± 1.13 h) ($t = 3.04$, $df = 14$, $P = 0.009$) (Figure 9). No significant difference was found in mean oviposition start time for females that had no copulation (1711 ± 3 h 24 min), short copulation (1751 ± 2 h 58 min), or long copulations (1818 ± 2 h 29 min) (ANOVA, $F = 0.057$, $df = 2, 20$, $P = 0.945$). No significant differences were found when comparing oviposition statistics between females in the three categories (Table 2). These results indicate that the type of copulation experienced preceding oviposition has no detectable effect on the timing of oviposition, the number of eggs a female lays, or the duration of time she spends ovipositing.

A struggle terminated 62.5 % of long copulations but only 16.7 % of short copulations ($\chi^2 = 2.94$, $df = 1$, $0.05 < P < 0.10$). I observed that males remove their genitalia prior to the start of the post-copulatory struggle about half of the time suggesting that they may initiate termination of copulations. However, I also observed males lunging at, and attempting copulation with the same female right after the post-copulatory struggle. By struggling, females effectively prevented males from guarding once they had lost genital contact.

Figure 9

Mean start times and durations of copulations, latencies to oviposit and oviposition for females categorized according to their last copulation before oviposition. White = duration of time from start of trial until start of the last copulation before oviposition or until oviposition in the case of females that did not copulate. Black = copulation duration. Hatched = duration of time between end of copulation and oviposition (latency to oviposit). Striped = duration of oviposition. Transition points between differently shaded areas (e.g. from hatched to striped) indicate mean start times for the behaviours. Data collected from focal observations of 23 independent females. Sample sizes for the three categories of copulation, long, short, and none were 12, 4, and 7 respectively.

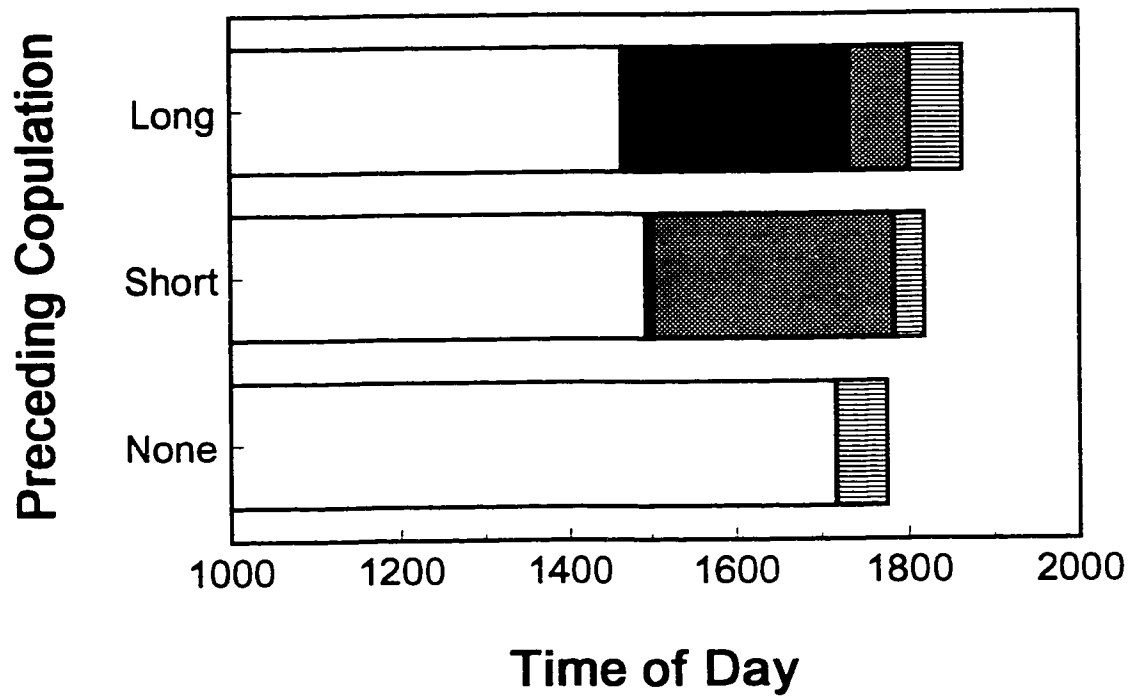


Table 2

Oviposition descriptive statistics (means \pm SD) for females categorized by the last copulation experienced before oviposition. Data from the focal observation experiment. Sample sizes are in parentheses. Time / bout = minutes spent ovipositing per bout; Total time = total number of minutes spent ovipositing during the trial.

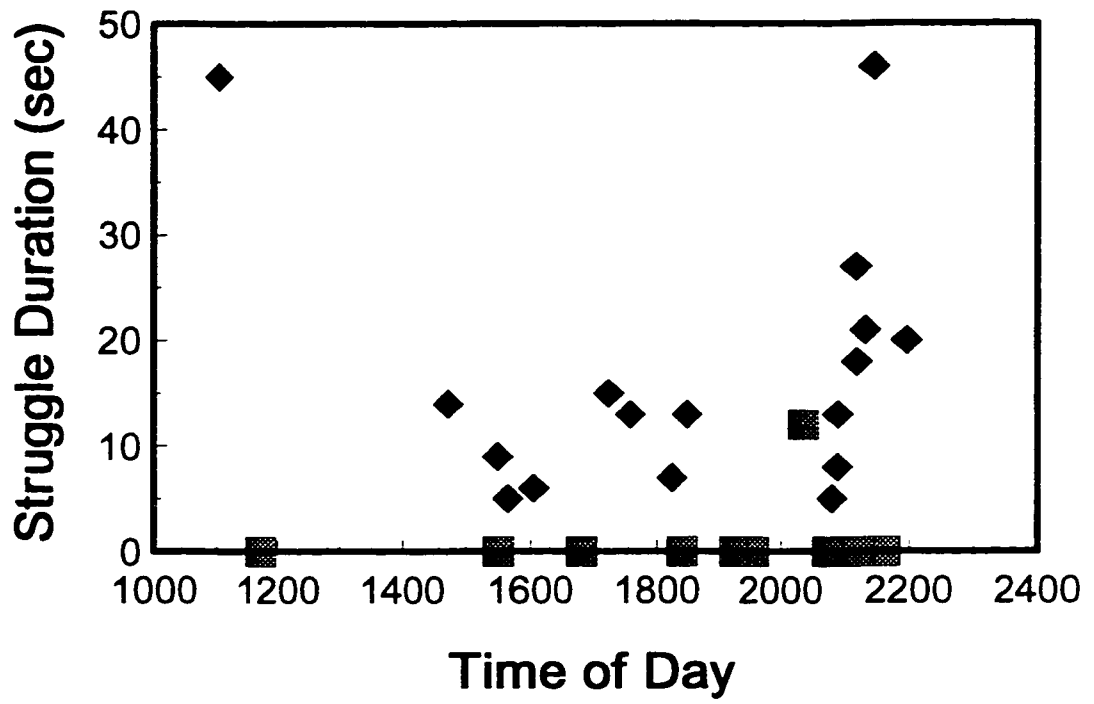
Variable	Preceding Copulation			χ^2	df	P
	Long	Short	None			
# Eggs Laid/ Trial	6.6 \pm 2.9 (5)	5.0 \pm 4.4 (4)	6.6 \pm 2.4 (4)	0.0297	2	0.9853
# Bouts / Trial	5.62 \pm 1.24 (13)	3.73 \pm 1.07 (11)	4.29 \pm 1.32 (7)	1.7948	2	0.4076
Time / Bout	9.35 \pm 2.84 (13)	7.43 \pm 1.74 (11)	11.35 \pm 6.72 (7)	0.1090	2	0.9469
Total Time	41.11 \pm 11.62 (13)	21.57 \pm 4.34 (11)	26.77 \pm 6.71 (7)	0.5541	2	0.7580

The duration of pre-copulatory struggles can be used as an estimate of a female's reluctance to mate. Previous research has shown that female reluctance depends on male density and consequently intensity of male harassment (Krupa and Sih 1993; Sih and Krupa 1995). My study indicates that a female's readiness to oviposit may also affect her level of reluctance to mate. Copulations occurring before oviposition began with a pre-copulatory struggle 94 % of the time where as copulations following oviposition began with a pre-copulatory struggle only 9 % of the time ($\chi^2 = 21.15$, df 1, $P < 0.001$).

Females from the focal observations that copulated before and after oviposition were used in a paired t-test comparing pre-copulatory struggle durations. Pre-copulatory struggles before oviposition were on average 8 ± 3 sec in duration while those following oviposition were 2 ± 2 sec in duration. Since only six females copulated both before and after oviposition no statistical significance was found ($t = 2.17$, df 5, $P = 0.082$). A non-paired t-test that allowed the inclusion of females that copulated either before or after oviposition provided more power. Only one female from each trial was used in this analysis and each female was used either in the before or after oviposition category (29 females in total). Females that copulated both before and after ovipositing were alternately placed into one of the categories. Females which oviposited within 2 h after their trial were included in the before oviposition category. This comparison revealed significantly longer pre-copulatory struggles before oviposition than following oviposition (Mann-Whitney U test, $U = 12.0$, $n = 11,18$, $P = 0.0001$) (Figure 10). The mean duration of pre-copulatory struggles before oviposition was 16 ± 3 sec and after oviposition 1 ± 1

Figure 10

Pre-copulatory struggle duration as a function of time of day. Diamonds = pre-copulatory struggles occurring before oviposition; squares = pre-copulatory struggles occurring after oviposition. Each data point represents one female from the focal observations.



sec. The durations of pre-copulatory struggles occurring before oviposition were not correlated with time of day ($r = -0.037$, $df 18$, $P = 0.885$). Upon removing the two outliers, the correlation was close to significant ($r = 0.460$, $df 16$, $P = 0.073$), but in the opposite direction from that expected if time of day was causing the reduction in female reluctance to mate from before to after oviposition. Thus, it seems that the act of oviposition, not time of day causes the shift in female reluctance to mate.

If harassment was causing this change in female reluctance we would predict greater harassment levels after oviposition. I compared levels of harassment experienced by eight females that had oviposited to those experienced by eleven females that oviposited after the trial. Harassment was quantified as duration and number of struggles that did not result in copulation. I divided the trial into three 4 h time intervals to see whether the number of struggles experienced by females was greater at any one time of the day. A multivariate repeated measures ANOVA was performed with the within subject factor being mean number of struggles at the different time intervals, and a between subject factor being whether the female oviposited during the trial or not. The analysis showed that 1) there was no significant difference in the number of struggles experienced during the trial between females that oviposited during the trial and those that did not ($F = 0.010$, $df 1, 17$, $P = 0.923$), 2) harassment did not vary significantly over time ($F = 0.852$, $df 2, 16$, $P = 0.445$), and 3) whether a female oviposited during the trial did not influence the temporal pattern of harassment ($F = 0.987$, $df 2, 16$, $P = 0.394$). No significant difference was found in mean struggle duration between females that oviposited (7 ± 1 sec) and

those that did not (8 ± 1 sec) ($t = 0.70$, $df 16$, $P = 0.494$). Therefore, there is no evidence that females experienced more harassment after oviposition.

Other than reluctance to mate, a female's readiness to oviposit had little effect on mating interactions. Females that oviposited during the trial had on average 3.4 ± 0.8 copulations while those that did not oviposit had on average 3.3 ± 0.5 copulations ($t = -0.04$, $df 28$, $P = 0.965$). The proportion of copulations that were long in duration was 51 ± 9 %, and 65 ± 10 % for females that oviposited and those that did not respectively ($t = 0.99$, $df 28$, $P = 0.330$). The proportion of copulations that were long occurring just before oviposition (63%) was not significantly different from the proportion occurring just after oviposition (86%) ($\chi^2 = 0.18$, $df 1$, $P > 0.75$).

Discussion

This is the first study to investigate oviposition behaviour in the context of sexual conflict in a waterstrider species. The results indicate that several aspects of oviposition behaviour may contribute to sexual conflict in *A. remigis*. These aspects include the act of oviposition, the number of eggs laid, the daily rhythm of oviposition, and the association between a female's readiness to oviposit and her reluctance to mate.

The act of oviposition may contribute to sexual conflict in two ways. First, females tend to search for oviposition sites and oviposit well below the surface of the water making them unavailable for mating. Oviposition thus shifts the sex ratio of reproductive individuals towards males and consequently alters the intensity of sexual selection on males (Rowe 1992; Krupa and Sih 1993; Sih and Krupa 1995; Fairbairn and Preziosi 1994; Arnqvist 1997). Underwater oviposition has been reported in *A. remigis*' sister species in Europe, *A. najas* which is also stream-dwelling (Sattler 1957 as cited in Andersen 1982; Brinkhurst 1960). However, unlike the characteristic backwards descent on a substrate by *A. remigis* females, *A. najas* females dive down for underwater oviposition (Sattler 1957 as cited in Andersen 1982). Most other Gerridae species are pond-dwellers and lay their eggs on the underside of floating vegetation (Andersen 1982; Hayashi 1995). The females of these species, unlike those of *A. remigis*, are visible to males while searching for oviposition sites and hence are available for mating attempts.

The second way in which the act of oviposition may contribute to sexual conflict in *A. remigis* stems from the fact that females only oviposit while solitary. They prevent mates

from post-copulatory guarding by vigorously struggling, but do not usually oviposit immediately after the termination of copulation. Thus, the potential for remating between copulation and oviposition combined with last male sperm precedence means that insemination does not guarantee fertilization in this species. This situation does not arise in *A. najas* because males continue to guard their mates after the loss of genital contact (Sattler 1957 as cited in Andersen 1982). These males remain on the backs of their mates even while they dive underwater for oviposition (Sattler 1957 as cited in Andersen 1982).

The number of eggs that females lay is another aspect of oviposition behaviour which may contribute to sexual conflict in *A. remigis*. Females lay relatively few eggs each day (Fairbairn 1988b; Blanckenhorn 1991; Blanckenhorn and Fairbairn 1995; Blanckenhorn et al. 1995; Preziosi and Fairbairn 1997). The number of mature eggs females carry, however, is greater than the number of eggs they lay per day (Fairbairn 1988a; Preziosi et al. 1996). In addition, during a bout of oviposition females generally lay one to two eggs and then resurface before the next bout. Thus, females may remate between bouts of oviposition as well as between oviposition on different days. High levels of sperm competition may result from this oviposition behaviour. Because females tend to mate several times per day, from any single mating, a male can expect fertilization precedence for only a small fraction of the female's mature eggs. The females of most other Gerridae species lay their eggs in groups (Spence 1986; Nummelin et al. 1988; Hayashi 1995) and in the species *A. elongatus* it is known that the females lay all of their mature eggs each time they oviposit (Hayashi 1995). Therefore, it seems likely that *A. remigis* males sire

fewer offspring per mating than males of other Gerridae species.

The daily rhythm of oviposition may contribute to sexual conflict in *A. remigis*. In the presence of males (1:1), rates of oviposition were lower than average in the morning, higher than average in the afternoon, peaked in the early evening just prior to “lights out” or dusk, and continued higher than average for the first few hours of darkness. A similar pattern has been found in several diurnal insect species (e.g. Loher and Chandrashekar 1970; Shaerer et. al. 1995). Peaks in oviposition rhythms tend to coincide with dusk, and in some species a second peak coincides with dawn (e.g. Tessmer et. al. 1995). Temperature change was not required for the daily rhythm in oviposition to occur since the pattern observed in the field also occurred in the laboratory in the absence of temperature cues.

The absence of males significantly altered the daily rhythm in oviposition. Females oviposited at lower rates over a longer span of light hours and very little during dark hours. The two treatments (males present or absent) in the scan sampling experiment differed in density as well as sex ratio but the altered rhythm in the absence of males was not due to the reduction in density (43 to 21 waterstriders / m²). The preliminary experiment and field scan sampling (19 and 9 waterstriders / m² respectively) were even lower in density but showed the same pattern of oviposition as the males present treatment. Therefore, it was likely the absence of males, not the change in density that altered the daily rhythm of oviposition.

The effect of males on the daily rhythm of oviposition was not due to females delaying

oviposition because of prolonged copulation. Females initiated oviposition around the same time of day regardless of their copulation history. Egg fertilization most likely occurs just before oviposition (Andersen 1982). Thus, delayed oviposition may produce conflicts of interests between the sexes when females mate multiply because the intensity of sperm competition would be increased (Birkhead and Møller 1993a & b). On average, females had two long copulations between 1000 and 2200. Sperm transfer is believed to occur during long copulations and therefore the sperm from the different males had to compete for fertilization precedence. Whether females can exert some form of internal control over paternity remains unknown for this species. Birkhead and Møller (1993a) hypothesized that in species where females are forced to copulate, or copulate out of convenience such as *A. remigis*, internal control of paternity may be more adaptive than external control.

The final aspect of female oviposition behaviour which may contribute to sexual conflict in *A. remigis* is the relationship between a female's reluctance to mate and her readiness to oviposit. Using pre-copulatory struggle duration as a measure of female reluctance illustrated that females are more reluctant to mate just prior to oviposition than following oviposition. An alternative method for quantifying female reluctance is to rank pre-copulatory struggles by the number of resistance moves the female makes (Lauer et. al. 1996). I did not quantify pre-copulatory struggles this way, but 91 % of females showed no resistance to mating attempts after oviposition whereas before oviposition only 6 % of females showed no resistance to mating attempts. Therefore, regardless of the

method used the same result is obtained. There was no evidence that the intensity of male harassment experienced by females was higher after oviposition and therefore the change in female reluctance seems to be related only to their readiness to oviposit. Female damselflies of the species *Enallagma hageni* have also been found to alter their reluctance to mate according to their readiness to oviposit (Fincke 1988). These females, however, are less reluctant to mate prior to oviposition than after (Fincke 1988). Males guard their mates from the harassment of other males while they oviposit (Fincke 1988). Thus, in this damselfly species, mating facilitates oviposition, rather than the reverse as in *A. remigis*.

The association between a female's readiness to oviposit and reluctance to mate may cause daily changes in the intensity of sexual conflict. Just prior to oviposition the intensity of sexual conflict would be most intense. For males this would be the best time to mate because of last male sperm precedence and the short guarding period which would be required. However, for females it would be the worst time to mate because they only oviposit while solitary. After oviposition the intensity of sexual conflict would be reduced. By mating, females would experience reduced harassment by solitary males and therefore would be better able to forage, and gain nutrients for the production of mature eggs (Rubenstein 1984; Wilcox 1984; Blanckenhorn et. al. 1995). For males this would be the worst time to mate in terms of their probability of successfully fertilizing the female's eggs. However, males seem to be just as insistent to mate with females that have finished ovipositing as they are with females that have not oviposited. Hence, it is the relationship between a female's readiness to oviposit and her reluctance to mate that

changes the intensity of sexual conflict at different times of the day.

In conclusion, several aspects of oviposition behaviour contribute to sexual conflict in *A. remigis*. The act of oviposition and the low number of eggs laid per day increase the opportunity for sperm competition and produce selection favoring males that mate multiply. Delayed oviposition in the presence of males increases sperm competition because females may mate multiply before laying eggs. The association between a female's readiness to oviposit and her reluctance to mate alters the intensity of sexual conflict over the occurrence and duration of copulations at particular times of the day, and as a result, the intensity of sexual selection on males is expected to vary with time of day, being highest in the afternoon and evening when female reluctance is highest and they are close to oviposition, and lowest overnight and in the early morning. Thus oviposition behaviour contributes to sexual conflict in several ways and through its effects on the intensity and form (competition for mates, sperm competition) of sexual selection on males, plays an important role in shaping mating interactions in this species.

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