

The effects of operational sex ratio and food deprivation on copulation duration in the water strider (*Gerris remigis* Say)

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Summary. A North American water strider, *Gerris remigis* (Hemiptera) copulates for prolonged periods of time, apparently beyond the time necessary for insemination (Rubenstein 1984; Wilcox 1984; Clark 1987). I tested predictions from two different hypotheses of the adaptive significance of this behavior. Manipulations of the operational sex ratio in artificial “streams” revealed that water striders copulate significantly longer when the sex ratio is male-biased. This result is consistent with the hypothesis that prolonged copulation functions as a type of contact mate guarding, which reduces sperm competition by preventing the female from remating prior to oviposition. The finding is also consistent with the hypothesis that copulation is prolonged to enhance female foraging efficiency. In a second experiment, sex ratio and total population density were held constant, and the period of food deprivation of females was manipulated. Contrary to the predictions of the female foraging hypothesis, “starved” females did not copulate longer than “fed” females. Of the two hypotheses considered, only the copulatory guarding hypothesis explains both results. This does not mean, however, that there is no selective benefit from the enhanced foraging efficiency resulting from prolonged copulation. Nor does it exclude the possibility that this benefit has been necessary for the evolution of prolonged copulation in water striders.

Introduction

Prolonged copulation represents a paradox in sexual selection theory. Although energetic and temporal constraints usually limit a female’s reproductive success to the number of gametes she can pro-

duce, male success is most often limited by the number of inseminations males achieve (Trivers 1972). This leads to intra-male competition for females, and should select for males which minimize the amount of time necessary to find, court, and inseminate a female, thereby achieving the maximum fertilization rate (Parker 1974).

How then do we explain prolonged copulation? Males sometimes copulate longer than necessary to complete insemination (e.g. brimstone butterflies, Labitte 1919; houseflies, Murvosh et al. 1964; and walkingsticks, Thornhill and Alcock 1983). The most widely accepted hypothesis is that prolonged copulation functions to reduce or eliminate sperm competition – the competition to fertilize ova occurring inside the female’s reproductive tract between stored ejaculates of different males (Parker 1970). By remaining *in copula*, a male prevents subsequent males from mating with the female and thereby diluting or displacing his sperm. Viewed this way, prolonged copulation functions as a form of copulatory mate guarding (copulatory guarding hypothesis).

This hypothesis has been widely accepted. Thornhill (1984) has recently argued, however, that biologists are prone to dwell on this hypothesis unduly, to the neglect of other alternatives. Indeed, recent research has shown that prolonged copulation, in some species, is not functioning just as a form of copulatory mate guarding (e.g. Dickinson 1986; McLain 1980). Moreover, Walker (1980) has noted that researchers have tended to focus solely on the male’s evolutionary interests and that some traits, commonly accepted to be sperm competition avoidance mechanisms, may have evolved as a result of sexual selection by females.

In the water strider, *Gerris remigis* Say, prolonged copulation may confer a selective advan-

tage by increasing female foraging efficiency (female foraging hypothesis). Female *G. remigis* copulate and forage in the same areas, often concurrently. Wilcox (1984) observed water striders foraging in laboratory tanks and measured the average duration of mating attempts by males when grasping single females and copulating pairs. The average "grasp time" on single females was 16.4 ± 12.3 seconds, but only 1.0 ± 0.3 seconds for mated pairs (Wilcox 1984). Thus, paired females wasted less foraging time repelling mating attempts. In addition, Rubenstein (1984) found that in the wild, copulating females were subject to significantly fewer attacks than when they foraged in the same area unpaired. In the laboratory, single females foraging with no males present detected 100% of simulated prey (styrofoam balls). Paired females detected only 85% (Wilcox 1984). However, when males were present, the detection rate by single females fell to 32%.

In the field, single females were found predominantly along the edges of pools when males were present (97% of single females) (Wilcox 1984). Foraging females were almost all copulating. Wilcox (1984) introduced a single male into 4 small pools, each of which contained a single swimming female. In all four cases, the female soon copulated. Wilcox concluded that when males were present, female *G. remigis* could forage efficiently only by being *in copula*.

In many insect species, the rates of oogenesis, vitellogenesis and oviposition are limited by the availability of nutrients (Chapman 1982; Engelmann 1970; Thornhill 1976). Thus, an increase in a female's foraging efficiency could be of direct benefit both to her own fitness and that of her mate. This is true even if prolonged copulation does not function to reduce sperm competition and the male fertilizes the same percentage of eggs as before. However, whether this increase in offspring will result in a net benefit to the male will depend on the relative magnitude of several parameters: the increase in the number of offspring he will sire by remaining *in copula* versus the probability that he could have found another mate during the additional time copulation was prolonged, times the expected number of offspring that he would have sired from the second mating.

Although both hypotheses predict that water striders should vary copulation duration as the relative costs and benefits of the behavior change, they differ in their assumptions as to which sex is controlling copulation duration. The copulatory guarding hypothesis assumes the male is regulating the duration of copulation in an attempt to maxi-

mize his fertilization rate. In contrast, the female foraging hypothesis implies that it is the female which manipulates copulation duration to increase her fecundity. My observations of copulating water striders suggest that both sexes are capable of terminating copulation. Additionally, the copulatory guarding hypothesis requires that there is sperm competition. The exact nature of sperm precedence is not known in *G. remigis*. However, the conditions which lead to sperm competition – sperm storage by females, and multiple mating by females prior to oviposition – are known to exist in this species (Clark 1987).

A prediction of the female foraging hypothesis is that copulation duration should vary in response to changes in parameters that affect a female's foraging efficiency and energetic requirements, such as the operational sex ratio and the number of eggs a female is carrying (Wilcox 1984). Variation in copulation duration with variation in operational sex ratio is also a prediction of the copulatory guarding hypothesis (Thornhill and Alcock 1983) since the costs and benefits to males of prolonged copulation depend on the probability of finding another receptive female and the likelihood that the current female will remate prior to ovipositing. Both hypotheses predict that mean copulation duration will increase when males outnumber females. However, although the female foraging hypothesis also predicts an increase in copulation duration when female energetic needs are greater (Wilcox 1984), the copulatory guarding hypothesis makes no such prediction. In fact, since energetically stressed females are of less reproductive value to the male (Boorman and Parker 1976), the copulatory guarding hypothesis might predict a decrease in copulation duration. Of course, this would depend on whether males are able to assess the nutritional states of females.

These predictions all depend on an untested assumption: that intra-individual variation in copulation duration is an adaptive response rather than random environmentally induced variation around some genetically determined duration. The goals of the research reported here were first to test this assumption, and then if copulation duration was found to vary as predicted by the hypotheses, to determine which hypothesis best explained the observed behavior.

Methods

Effect of OSR on copulation duration

The purpose of the first experiment was to test the effect of the operational sex ratio (independent variable), on copulation

duration (dependent variable). I created two "streams" by placing large, children's wading pools (diameter 1.5 m) in an outdoor enclosure, and filling these to a depth of approximately 15 cm. A pump created a circular current in both pools. The two operational sex ratios used in this experiment were 3:1 and 1:3 (males:females). The hypotheses were: H_0 : copulations do not last significantly longer when the sex ratio is male biased; and H_1 : when the operational sex ratio is male biased, copulations last longer than when it is female biased. The Kolmogorov-Smirnov two-sample procedure (Siegel 1956) was used to test for significance ($\alpha=0.05$ one-tailed).

The day before a trial, I collected wild *G. remigis*. Each animal was marked with a unique series of dots of colored Liquid Paper™ along its dorsum. Then I placed the animals in single-sex tanks and provisioned them with vestigial-winged *Drosophila*.

On the morning of a trial, I randomly assigned individuals to the two experimental groups. There were 12 animals in each group: nine males and three females in one group; nine females and three males in the other.

A trial began when I placed the animals in the two artificial streams. For the first trial, the experimental groups were assigned to the pools by a coin toss. I alternated the pool assignment in successive trials to avoid site bias.

I recorded to nearest minute the beginning of any copulation I saw. Copulations were classified as either "independent" or "non-independent". An independent copulation was defined as a copulation between two water striders, neither of which had copulated previously in the trial. By definition, there could be at most three independent copulations per pool per trial. I recorded all copulations I observed, but used only independent copulations in the statistical analyses.

A trial ended when any one of three conditions was met: 1) all possible independent copulations had ended; 2) 4.5 hrs had elapsed since the initiation of the trial and no independent copulations were currently in progress; or 3) all independent copulations had been monitored for a minimum of 4.5 h. Any independent copulations lasting ≥ 4.5 h were lumped in one time category. Any non-independent copulation in progress when observations were suspended, was eliminated from the data. Following the conclusion of a trial all animals were released. Four trials were performed.

Effect of female nutritional state on copulation duration

The purpose of the second experiment was to test the effect of female nutritional state (independent variable) on copulation duration. The experimental setup was the same as in the previous experiment, except that the pools differed in the nutritional state of the females rather than in sex ratio. The sex ratio in both tanks was 1:1. The hypotheses were: H_0 : starved females do not copulate significantly longer than fed females; and H_1 : starved females copulate longer than fed females. $\alpha=0.05$ (one-tailed).

The day before a trial animals were captured and marked. Then I placed all males in a single tank and provisioned them with vestigial-winged *Drosophila*. Females were randomly assigned to the two experimental groups, "fed" and "starved". I placed females in the starved group in a clean tank, tightly covered with fiberglass screening. I placed the fed group in a separate tank and abundantly provisioned them with vestigial-winged *Drosophila*. On the morning of the trial, I used a random number table to assign males to the two experimental groups. There were 5 males and 5 females in each pool. Trials were begun 24 hrs following the assignment to the experimental

groups. After food deprivation for this amount of time females defend food territories (Wilcox and Ruckdeschel 1982) and increase the average length of a feeding bout (Jamieson and Scudder 1977). The rest of the procedure was the same as in the first experiment.

Results

Effect of operational sex ratio on copulation duration

I observed a total of 44 copulations (Fig. 1) including 22 classified as independent (Fig. 2). As predicted, copulations were significantly longer when the operational sex ratio was male biased ($K_D=6$, $P=0.05$ one-tailed).

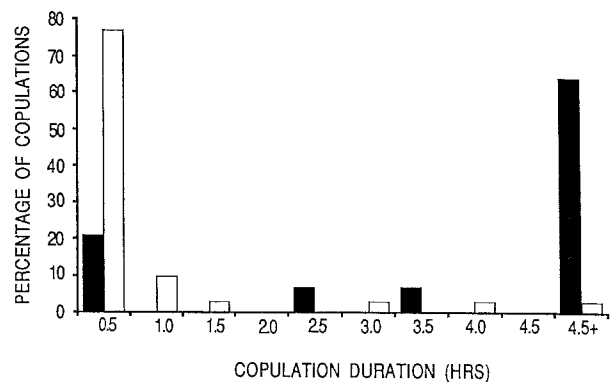


Fig. 1. Distribution of the durations of 44 copulations occurring in two artificial streams with different operational sex ratios (3:1 and 1:3). X-axis gives copulation duration in 1/2 h intervals. Y-axis gives the number of copulations in each time category, expressed as a percentage of the total number of copulations. Solid bars represent the male-biased group ($n=14$), open bars the female biased ($n=30$)

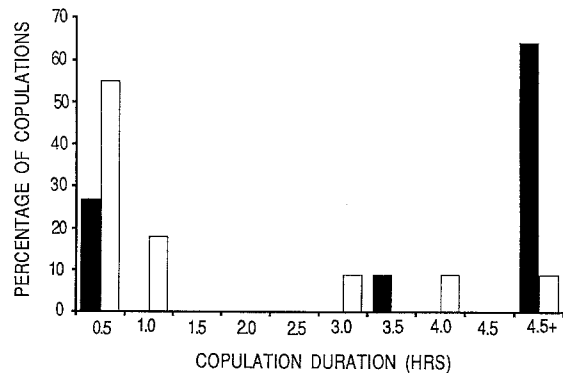


Fig. 2. Distribution of the durations of 22 "independent" copulations occurring in two artificial streams with different operational sex ratios (3:1 and 1:3). X-axis gives copulation duration in 1/2 h intervals. Y-axis gives the number of copulations in each time category, expressed as a percentage of the total number of copulations. Solid bars represent the male-biased group ($n=11$), open bars the female biased ($n=11$)

Effect of female nutritional state on copulation duration

I observed a total of 68 copulations (Fig. 3) including 27 classified as independent (Fig. 4). There was no significant difference in the distribution of copulation durations ($D=0.275$, $X^2=2.04$, $0.30 < P < 0.50$ one-tailed). On the basis of these results, the null hypothesis, that depriving females of food does not affect copulation duration, must be accepted.

Any time there is a failure to reject the null hypothesis, the possibility of a type II (β) error should be considered. It does not appear likely that the null hypothesis was falsely accepted for several reasons. Based on the results of the first experiment, the population "effect" size (γ) should

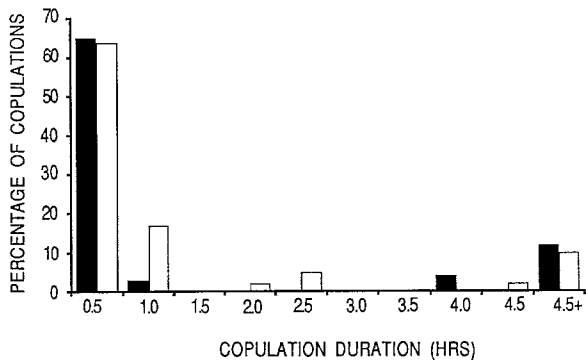


Fig. 3. Distribution of the durations of 68 copulations occurring in two artificial streams containing females on different nutritional regimens. The X-axis gives copulation duration in 1/2 h intervals. The Y-axis gives the number of copulations in each time category, expressed as a percentage of the total number of copulations. Solid bars represent the fed group ($n=26$), open bars the starved ($n=42$)

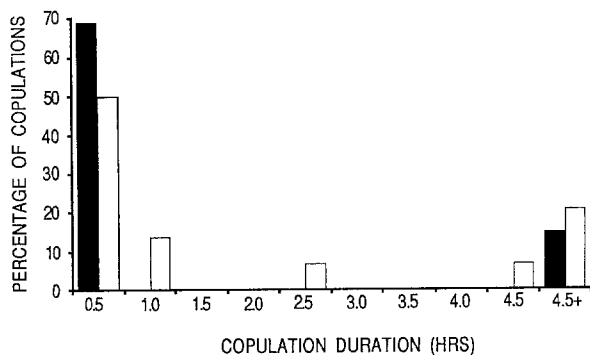


Fig. 4. Distribution of the durations of 27 "independent" copulations occurring in two artificial streams containing females on different nutritional regimens. X-axis gives copulation duration in 1/2 h intervals. Y-axis gives the number of copulations in each time category, expressed as a percentage of the total number of copulations. Solid bars represent the fed group ($n=13$), open bars the starved ($n=14$)

be large for this particular test. Additionally, the null hypothesis would not be rejected even with $\alpha=0.30$. Moreover, increasing the power of the test, by including both independent and non-independent copulations, does not lower the probability of the results ($n=68$, $D=0.179$, $X^2=2.06$, $0.30 < P < 0.50$ one-tailed).

Discussion

The results of the first experiment are the first demonstration that the duration of copulation in water striders varies in response to the operational sex ratio. These findings are consistent with the adaptive hypothesis that selection has affected the mean copulation duration, and that intra-individual variation in copulation duration is, at least in part, a response to changes in the costs and benefits of prolonging copulation.

These results also imply that water striders are capable of assessing the operational sex ratio. What behavioral mechanism might permit this assessment? Male water striders signal by vibrating their fore (prothoracic) legs on the water surface. In an elegant experiment Wilcox (1979) demonstrated that the presence of this signal is sufficient for sex recognition. The operational sex ratio could easily be obtained if water striders kept track of the number of conspecifics encountered and the number of those that rippled.

The results also indicate that the operational sex ratio assessment is updated on a regular basis. Although the distribution of copulation times was significantly different for the two experimental treatments, all subject animals had been drawn from the same stream, and had been kept in identical conditions until the start of the trial.

These findings are consistent with the predictions of both the "copulatory guarding hypothesis" and the "female foraging hypothesis". When males are relatively prevalent in the population, the probability that a male will find another mate if he terminates copulation decreases, and the chances go up that his current mate will remate prior to oviposition. Also when the ratio of males to females is high, harassment of foraging females will increase.

Since both hypotheses predict that copulation duration will vary with the operational sex ratio in the same fashion, a parameter had to be found that was experimentally controllable, and resulted in different predictions from the two hypotheses. Depriving some females of food and feeding others to excess fulfills this requirement. If males are varying the duration of copulation in order to maxi-

mize their paternity, the degree of hunger experienced by their mates should have little effect on copulation duration. If anything, the effect of increasing the level of hunger in females ought to be to decrease the duration of copulation, providing males can detect the condition of the female, since nutritionally deprived females should produce fewer eggs. However, if copulation is being prolonged to increase female foraging efficiency, then hungry females should copulate longer, since the ratio of costs to benefits associated with prolonging copulation is smaller for them than for sated females.

The results of the second experiment suggest that the duration of copulation is not varying in accordance with female foraging needs. There is no significant trend for "starved" females to copulate longer than the "fed" group.

Could the food deprivation period used have failed to induce a significant difference in hunger level between the two groups? I discount this possibility as previous work (Jamieson and Scudder 1977) has shown that 24 hrs of food deprivation is sufficient to significantly alter the feeding behavior of *G. remigis* and to cause individuals to defend foraging territories (Wilcox and Ruckdeschel 1982), yet is not so severe as to make females listless.

These results do not preclude the possibility that prolonged copulation enhances female foraging efficiency. The work of Wilcox (1984) demonstrates that prolonged copulation does indeed function in this capacity, at least in a laboratory setting. Furthermore, in the course of my research, I confirmed Wilcox's (1984) observations that, in the field, when males were present, virtually no single females were seen foraging. These results show that, whether or not prolonged copulation enhances female foraging, the female foraging hypothesis is not sufficient to explain the observed variation in copula duration. Only the copulatory guarding hypothesis fully accounts for the results of both experiments.

However, if the female foraging hypothesis is not sufficient to explain the observed variation in copulation duration in *Gerris remigis* it may still be relevant to understanding the evolution of prolonged copulation in this species. Knowlton and Greenwell (1984) developed a game theory model of the evolution of "sperm competition avoidance mechanisms". They found that avoidance mechanisms which are initiated following insemination can evolve regardless of whether they are beneficial or detrimental to female fitness. Using a recently developed set of ESS equations (Clark 1986), I

constructed a game theory model which showed that the evolution of post-insemination avoidance mechanisms may be quite difficult unless: 1) they are also beneficial to female fitness; or 2) there is some cost to females associated with prematurely terminating copulation (Clark 1987). The female foraging hypotheses could therefore be crucial for understanding the evolution of prolonged copulation in *Gerris remigis*.

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