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Janet E. Ruppert

*Eastern Illinois University*

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Mating behavior of the giant waterbug

Belostoma flumineum Say

(TITLE)

BY

Janet E. Ruppert

**THESIS**

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS  
FOR THE DEGREE OF

Master of Science

IN THE GRADUATE SCHOOL, EASTERN ILLINOIS UNIVERSITY  
CHARLESTON, ILLINOIS

1986

YEAR

I HEREBY RECOMMEND THIS THESIS BE ACCEPTED AS FULFILLING  
THIS PART OF THE GRADUATE DEGREE CITED ABOVE

7 Aug 1986  
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7 August 1986  
DATE

DEPARTMENT HEAD

The undersigned, appointed by the Chairman of the Department  
of Zoology, have examined a thesis entitled

MATING BEHAVIOR OF THE GIANT WATERBUG

Belostoma flumineum Say

Presented by

Janet E. Ruppert

a candidate for the degree of Master of Science  
and hereby certify that in their opinion it is acceptable.

## ABSTRACT

Sexual selection theory predicts that in the few species where males make a larger parental investment than females and limit female reproduction, females should court and compete for males (i.e. we should observe "sex-role reversal"--Trivers, 1972). These predictions were tested in the laboratory with the giant waterbug Belostoma flumineum Say (Hemiptera: Belostomatidae). Males of this species characteristically carry and brood eggs on their dorsa, thus making a substantial parental investment.

The courtship sequence in "one male:one female" pairings began with the male "pumping" (rapidly raising and lowering his abdomen at the water's surface). This presumably attracted the female, who then moved to and contacted the male. Placing his hind leg over the female's back, the male positioned the female and copulation occurred. Oviposition invariably followed. After the female deposited approximately four eggs, the male forced the female back to copulate again. This cycle continued virtually uninterrupted until the male was approximately 80% encumbered ( $\bar{X}$ =102 eggs).

"Two male:one female" trios were set up to simulate a situation in which access to females limited male reproduction. The same general courtship sequence was observed, with minor variations. The rate of male pumping (i.e. pumps per minute) was significantly higher than in

any other sex ratio situation observed. Oviposition frequently did not follow copulation. Both components of sexual selection appeared to be observed:

1) intrasexual selection was seen in males "striking" at each other, and 2) intersexual selection (i.e. courtship competition) was observed in male pumping displays.

A situation in which access to males limited female reproduction was simulated in "one male:two female" trios. Again, the same general courtship sequence was followed with minor variations. The rate of male pumping did not differ significantly from "one male:one female" pairings. Oviposition frequently did not follow copulation. Intrasexual selection was observed in the form of a "pushing" behavior, where one female would attempt to push another female off of the male's back. However, no intersexual selection (i.e. no female courtship) was seen. Thus what is observed may be "partial" sex-role reversal. Sex roles may rely as much on proximate circumstances as on pre-programmed genetic behaviors.

In order to assess preference for or dominance of partially-encumbered males and heavily-gravid females, additional trios were set up. Partially-encumbered males paired with unencumbered males and females did not breed significantly more than the unencumbered males. Heavily-gravid females paired with less-gravid females and males did breed significantly more than the less-gravid females. The manner in which these results relate to sexual

selection theory are discussed.

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## INTRODUCTION

In most species, males make a smaller investment in gamete production than females do. Their reproductive success is limited primarily by access to females (i.e. to eggs--Trivers, 1972). Thus, according to present-day sexual selection theory, their optimal reproductive strategy is to mate with as many females as possible (Trivers, 1972). Natural selection favors "mate quantity" in males.

In contrast, females contribute much energy in the production of gametes. Their reproductive success is limited primarily by the availability of resources or time (Trivers, 1972). Natural selection favors "mate quality" in females.

Darwin (1871) termed the differential reproduction which occurs due to non-random mating "sexual selection". Sexual selection has two components (Darwin, 1871; Huxley, 1938)--1) intrasexual, and 2) intersexual selection. Intrasexual selection involves competition between members of one sex (usually males) for access to members of the opposite sex. Intersexual selection, in contrast, involves an element of differential choice by members of one sex (usually females) for members of the opposite sex. In most species, males "advertise" some quality in the presence of a female, who then "selects" the male with which she will mate. These are considered to be traditional sex roles.

Gametic production is not the only consideration in determining sexual "roles". Trivers (1972) suggests that one must consider the total "parental investment", which he defines as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring". Production of gametes, as well as any post-copulatory parental care, would be included in this definition. Thus Trivers (1972) proposes that individuals of the sex with the least parental investment will compete among themselves to breed with members of the sex that invests more.

In most species, post-copulatory parental care is performed by the female (Thornhill and Alcock, 1983). In the few species where males make the larger parental investment, we should expect males to be the discriminating sex (Trivers, 1972). If males also become a limiting resource to female reproduction, we should see females courting and competing for males (i.e. we should observe "sex-role reversal"--Trivers, 1972; Thornhill and Alcock, 1983). Previous observations with insects (Cullen, 1969; Smith, 1979b; Gwynne, 1981; Venkatesan, 1983), pipefish (Takai and Mizokami, 1959), seahorses (Fiedler, 1954; Strawn, 1958), birds (Lack, 1968; Jenni, 1974; Oring et al., 1981; Reynolds et al., 1986) and others lend support to this theory.

The giant waterbugs (Hemiptera: Belostomatidae:

Belostomatinae) are appropriate subjects for sexual selection studies: males characteristically carry and brood eggs on their dorsa (Lauck and Menke, 1961), which is vital to egg-nymph survival (Cullen, 1969; Smith, 1976b; Venkatesan, 1983). Belostoma flumineum (used in this study) are approximately three centimeters long with an oval, flattened brown body, ciliated flattened hind legs, raptorial front legs and retractile air-straps (Cummings, 1933). They are generally associated with emergent vegetation in ephemeral and permanent ponds throughout the continental United States (Smith, 1976a). Smith (1976a) describes them as predaceous carnivores, feeding primarily on aquatic invertebrates.

Torre Bueno (1906) described the life-history of the waterbug. Adults overwinter in ponds. Oviposition begins in the spring, and continues throughout the summer. Incubation averages from 6 to 12 days. The young develop through five nymphal instars, with the first young-of-the-year adults emerging in June in Illinois (Kruse, unpubl. data).

Male B. flumineum appear to make a substantial investment in brooding their offspring (see Smith, 1976b, 1980). If this investment is larger than that of females, sexual selection theory predicts that females will court males, which should be the discriminating sex (Trivers, 1972). This assumes that males somehow limit female reproduction. To determine if this is actually the case,

one needs to consider the "operational sex ratio" (OSR), which is defined as the "average ratio of fertilizable females to sexually active males at any given time" (Emlen, 1976). Kruse (pers. commun.) is presently investigating various factors influencing the OSR in B. flumineum. VanDenburgh (1985) and Kruse (unpubl. data) have collected data suggesting that male backspace availability does limit female reproduction early (May and June) in the breeding season in Illinois.

In accordance with these data, sexual selection theory predicts that B. flumineum males should be courted by and competed for by females early in the summer (Trivers, 1972). In late June and July when the young-of-the-year emerge as adults (Kruse, unpubl. data), males should no longer be limiting, and traditional sex roles should be observed (i.e. females should be courted by and competed for by males).

I tested these courtship predictions in the laboratory. "One male:one female" pairings were set up, and courtship, mating and oviposition behaviors were described. Using these results as a "control" behavior, I manipulated the sex ratio in favor of either males or females, and attempted to determine any differences in courtship behavior.

## METHODS

In May-August 1985 and 1986, giant waterbugs (Belostoma flumineum) were collected from various ponds in Coles County in east-central Illinois (U.S.A.). Adult bugs, collected using aquatic insect nets, were transported to the laboratory in plastic coolers containing pond water and floating vegetation (e.g. sticks, cattails). In the laboratory, individual bugs were placed in covered, plastic containers (15 cm X 15 cm X 20 cm) containing aged tap water, gravel and plastic vegetation. Each individual was marked with an identification number on its pronotum, using white india ink covered with a thin layer of superglue. Bugs were fed dragonfly naiads and/or crickets ad libitum. Females were identified by the presence of two tufts of setae located mesally near the apical margin of the genital plate; males lack these setae (Menke, 1960).

### Aspect I: Mating Behavior

Bugs were maintained under a reversed (14L:10D) photoperiod. All behavioral observations were made under a red light, which allowed me to move around with no apparent disturbance to the bugs. A Sony video camera with a standard zoom lens and a video-cassette recorder were used to film behaviors.

All subjects were isolated for no less than one week after capture before being used. Sexually-mature adults were used, as determined by their body and eye color and size. Newly-emerged adults are relatively thin, having soft, green bodies with red eyes. In contrast, adults are more robust with brown body color and dark eyes. Two pairings of one male with one female were made as a control. Four matings of two males with one female and five trios of one male with two females were observed. Gravid females were used in matings, as determined by the degree of "rotundness" of their abdomens. (Female body size has been shown to be strongly positively-correlated with fecundity in many insects--Thornhill and Alcock, 1983.) Males which had been observed to "pump" (to be described) were also used in matings.

Data collected included:

- 1) pump duration (seconds)--each sequence was timed for as long as the male pumped, up to a five minute period,
- 2) pumps per minute--one pump consists of the male rapidly raising and lowering his abdomen three times, followed by a short pause;
- 3) copulation time (minutes)--measured from when the pair stops all visible movement to when the male moves, breaking up copulation,
- 4) oviposition time per egg (minutes)--measured from when the female stops all visible movement to when the female moves,

- 5) number of eggs oviposited per oviposition bout,
- 6) which of two males a female moved to with respect to:
  - a) which male was closer to the female,
  - b) which male exhibited a greater number of pumps/min,
- 7) number of times the female moved to a pumping male with respect to whether:
  - a) copulation occurred, or
  - b) the female moved away, or
  - c) the male moved away,
- 8) number of times the male moved away from the female, and the female:
  - a) subsequently returned to the same male, or
  - b) moved to the other male,
- 9) number of times the female moved to a pumping male with respect to whether:
  - a) the male slowed/stopped or continued pumping,
  - b) the female stayed with that male or moved to the other pumping male,
- 10) number of copulations with or without oviposition following,
- 11) number of oviposition attempts with respect to:
  - a) whether the second male/female competed,
  - b) whether the same male/female or the "intruding" male/female received eggs/oviposited after copulation,
- 12) number of times oviposition occurred without copulation immediately preceding,
- 13) general location of egg deposition (e.g. posterior,



- near head),
- 14) number of males with eggs from more than one female,
  - 15) number of females with eggs on more than one male,
  - 16) signs of physical aggression.

#### Aspect II: Mating Preference

Smith (1979a) has suggested that females of Abedus herberti prefer to mate with males already bearing a small clutch of eggs. In order to test if this is true for B. flumineum, I set up trios of two males with one heavily-gravid female. One male had no eggs; the other possessed a partial clutch of approximately 50 eggs (50% encumberment). Trios were left together for approximately one week, or until the female encumbered (i.e. oviposited on) one of the males. The number of eggs on each male and which male became encumbered were recorded.

Some of the males used in these trios were fully-encumbered males whose pads were artificially cut down to 50% of the original size. This was accomplished using a scalpel: the egg pad was loosened to the point of removal by sliding the scalpel between the pad and the hemelytra. Very gently, the pad was sliced between eggs. Then, exerting very gentle pressure downward, the loosened portion of the egg pad was pushed anteriorly until it was freed. In all cases, the posterior portion of the pad was

retained on the male, since females almost always encumber males from back to front (pers. observ.).

Since male brooding costs are fixed regardless of how many eggs the male carries, it is to the male's advantage to maximize the number of eggs in a clutch (Smith, 1979a). Thus males might prefer to mate with females that are heavily gravid over those that might only be able to give them a partial clutch. To test this hypothesis, I set up trios of one male and two females. One female was heavily gravid, as determined by the rotundness of her abdomen and the number of days since she last oviposited. The other female was less rotund and/or had oviposited more recently.

All females were weighed daily with an analytical balance. Exceptional weight loss and reduction in rotundness were used as indicators as to which female oviposited. In order to alleviate any extraneous weight change while mated, these trios were deprived of food for a maximum of one week. After this, males and females were separated and fed ad libitum for two days, after which trios were re-formed. Eggs resulting from these trios were counted and preserved. Both females from five mated trios were killed and dissected, and the number of eggs within each were recorded. The females which did not breed from five other trios were remated with two males. The number of days before these females bred was recorded.

## RESULTS

### Aspect I: Mating Behavior

In two "one male:one female" pairings, mating behavior began with the male "pumping". This consisted of the male rapidly raising and lowering his abdomen at the water's surface, averaging 15.5 pumps per minute (Table 1). Pumps per minute were calculated using the number of pumps per pumping sequence.

Females responded by moving to and contacting the male's body at any point, usually with one of her legs. The male then positioned the female, and copulation occurred. In positioning, the male brought his hind leg which was nearest the female over the female's back and positioned her at a right angle to himself. The male then lowered his abdomen, creating a gap between the abdomen and the hemelytra. Again using the same hind leg, the male maneuvered the apex of the female's abdomen into the gap, keeping her at a right angle to himself, and copulation occurred (Figure 1).

Copulation averaged 2.7 minutes (Table 1). This time was similar for all three sex-ratio situations.

Invariably, oviposition followed copulation: immediately after copulation ended, the female positioned herself over the male's dorsum. The first egg, always oviposited near the posterior end of the dorsum, was "cemented" via a

mucilaginous substance to the male's back. Each subsequent egg was laid adjacent to the others, working anteriorly (Figure 2).

Generally, three or four eggs were laid ( $\bar{X}=3.9$ ), averaging 1.0 minutes per egg in all mating situations (Table 1). After this, the female attempted to continue to oviposit. However, the male would not allow her to do so. Instead, he used his hind leg as before, pushing the female back to copulate again. This cycle continued virtually uninterrupted until the male's back was 80%-85% full ( $\bar{X}=102$  eggs). (See Table 3 for data on individuals. See Figure 3 for a summary of events.)

When two males were placed with one female, the general sequence of events as described for one-to-one matings occurred, with minor variations. Males were observed to exhibit "pumping displays", where both males pumped simultaneously. The female usually moved to the male that was closer to her, or to the male performing the most pumps per minute (17 times of 34 (50%) and 10 times of 34 (29%), respectively).

The number of pumps per minute was significantly higher (t-test;  $p=0.0000$ ,  $p=0.0001$ ) in "two male:one female" trios than for "one male:one female" or "one male:two female" matings, respectively, averaging 28.1 pumps per minute (Table 1, Table 2--see Table 4 for individual data).

Generally (83 of 95 times, 87%), once male-female

contact was made, pumping by that male decreased or ceased altogether as the male began to position the female. If the other male continued pumping, the female usually (33 of 40 times, 82%) left the first male and moved to the second. This changing of partners often continued to the point where very little copulation or oviposition actually took place. Out of four such trios, a mean of approximately ten eggs per mating was observed, as opposed to a mean of 102 eggs in the "one male:one female" situations.

Pumping displays occurred before any initial copulation (see Figure 4, pt. A). However, once copulation or oviposition occurred, pumping displays were still observed. Mating may have been interrupted at any point in the sequence.

When the female moved to a male, the male often moved away (48 of 106 times, 45%) and pumped again. The female returned to the same male 29 of 42 times (69%).

After copulation, oviposition usually (21 of 36 times, 58%) occurred without interference from the other male. Three of 36 times (8%), oviposition occurred after competition (in the form of pumping) from the other male. Occasionally (10 of 36 copulations, 28%) after copulation, either the male or the female moved away (without any obvious sign of competition), and no oviposition occurred. Two times (0.5%) no oviposition occurred, apparently due to competition from the second male.

On one of 25 oviposition bouts (4%), six eggs were

laid. On four occasions (16%), eggs were not laid posteriorly, but were laid anteriorly or medially on the male's back. These ova were soon knocked off or fell off. On one occasion, a male received five eggs from a female who had copulated with another male since mating with him.

Actual physical aggression between males was observed on seven occasions; in these situations, one male seemed to physically strike another male, essentially "jumping" at him and recoiling. This occurred only when the males pumped in very close proximity to each other (up to five centimeters). In all four trios, the female copulated with both males. In two of those cases, the female oviposited on both males.

When two females were placed with one male, the same general sequence of events as the control was again observed. However, there were some variations. Male pumps per minute were similar to those in "one male:one female" pairings ( $\bar{X}=12.96$ --Table 2; see Table 5 for individual data).

Females were observed to "push" each other, primarily after copulation and before oviposition (see Figure 4, pt. B). When one female was copulating, the other was always motionless. However, after copulation, the second female often (18 of 42 times, 42.9%) attempted to "push" the other female off of the male's back. Only three of the 18 times (17%) did the "aggressive" female succeed in displacing the first female and oviposit. Seven times (39%), the same

female that copulated oviposited. The remaining eight times (44%), neither female oviposited, with one to all members of the trio scattering. The male appeared very passive during these bouts, not seeming to aid or hinder either female. Females were also observed to "push" each other after the male pumped (see Figure 4, pt. C).

Three times out of five (60%), the male received eggs from both females. On two occasions (in the same trio), both females simultaneously oviposited on the male. Both females had previously copulated with that male. However, the "dominant" female competed and succeeded in laying two eggs before ever copulating with the male.

On two occasions, eggs were laid near the male's head rather than posteriorly. On one occasion, a female was observed to oviposit one egg on the back of another female. This female had just copulated with the male, who still had no eggs. The second female "pushed in" after copulation and oviposited on the male, while the first female oviposited on the second. Kruse and Leffler (1983), upon observing a field-captured female carrying four eggs, suggest that this might have resulted when two females were attempting to oviposit on the same male; my results confirm this speculation.

#### Aspect II: Mating Preference

Partially-encumbered males became further-encumbered nine times of 17 (53%), with the unencumbered males remaining unencumbered. This was not found to be statistically significant ( $\chi^2=0.4897$ , d.f.=1,  $p>0.05$ --Table 6). Two of those nine times (22%), the initial egg pad was dropped unhatched before a new clutch of eggs was deposited. On one occasion (14%), the partially-encumbered male's pad was dropped, but he did not receive any new eggs. Unencumbered males received eggs four of 17 times (24%). Both males received eggs four times of 17 (24%). See Table 6 for individual results.

In all cases, the heavily-gravid female oviposited eggs on the male (as determined by weight loss). As expected, all of the sacrificed heavily-gravid females had a total egg count exceeding that of the lighter females (Table 7). One remated female deposited 104 eggs on a male the next day (Table 8).



## DISCUSSION

### Aspect I: Mating Behavior

The giant waterbug Belostoma flumineum is an appropriate subject to test sexual selection theory: males make a large investment in brooding eggs--possibly more investment than the female. In addition, field data collected over three years show that, at least in some ponds, male backspace limits female reproduction early in the summer (Kruse, unpubl. data). Thus it is reasonable to predict that B. flumineum may show a type of sex-role reversal in courtship behavior.

All trios (two males with one female, and one male with two females) observed in the laboratory followed the same basic courtship sequence as the "one male:one female" controls. In all pairings, mating behavior began with the male "pumping". This presumably functions to attract females, since females responded by moving to and contacting the male. This might be interpreted as intersexual selection: males "advertise" and females "choose". That females choose to mate with pumping males is evident in observations of "display pumping" in the "two male:one female" matings: when male-female contact was made and pumping ceased, the female usually (77%) moved to another male that continued pumping.

What do females find "attractive" about a male's

ability to pump? Pumping may have once been a brooding behavior that has since been lost in B. flumineum. Smith (1980) reports that Abedus herberti, which inhabit flowing streams, exhibit brood-pumping below the water's surface, circulating water over their eggs. This is thought to renew the oxygen supply and disperse accumulated metabolic wastes (Smith, 1976a). Abedus herberti also pump during courtship, at a rate approximately ten times faster than that for brood-pumping (Smith, 1980). Smith (1979a) theorizes that females choose males demonstrating the ability for sustained pumping, indicating that they will be effective brooders.

Perhaps at one time, common ancestors to modern Abedus and B. flumineum also brood-pumped. In adapting to a more static environment, Belostoma may no longer have needed all six legs to hold on to substrate (Smith, 1980). With the hind legs free, brood-stroking behavior could now have evolved, and the brood-pumping behavior may have been lost. (Brood-stroking consists of the male brushing his hind leg over the eggs, anterior to posterior.) Perhaps brood-stroking created less disturbance to the water's surface than brood-pumping, decreasing the chance of detection by predators. Thus brood-stroking may have had a selective advantage over brood-pumping, in terms of parent-survival.

Females of B. flumineum occasionally (29.4%) appeared to choose males with greater pumps per minute over "slower" males. Natural selection may no longer favor males

demonstrating efficient brooding ability, as in Abedus. However, sexual selection may still favor this behavior. In "two male:one female" trios, males displayed a rate of pumping more than double that in either situation with a single male. It appears that, where males are scarce, females will mate with whatever male is available. Where males are abundant, females appear to require more display.

In "one male:one female" matings, oviposition invariably followed copulation. However, this was not the case in the trios: In "two male:one female" and "one male:two female" trios, oviposition followed copulation only 24 of 36 times (67%) and ten of 18 times (56%), respectively. This was due primarily to interference from the "extra" male or female. Occasionally (10 of 36 times, 28%), either partner in "two male:one female" trios moved away before oviposition, with no obvious sign of competition.

In all three mating situations, after ovipositing approximately three or four eggs, the female attempted to lay even more eggs. However, the male would not allow it, forcing an additional copulation before each oviposition bout. Smith (1979b) suggests that repeated copulations by the male insure that his sperm are used in fertilization, and not stored sperm from the female's spermatheca (i.e. repeated copulations assure the paternity of the eggs the male must brood--Smith, 1979b). Smith (1979b) believes this may assure paternity even under the most confusing

conditions of multiple matings.

This assurance is particularly important to males in situations where a female mates alternately with several courting males. Evidence indicates that sperm from the last male to copulate will be used in fertilization (Parker, 1970; Smith, 1979b). This makes it very easy for a male to be "cuckolded" if he does not take measures to assure his paternity. The process of natural selection should operate in such a way that anti-cuckoldry tactics evolve (particularly in species where males contribute a substantial amount of parental care), since brooding another male's eggs would decrease the relative fitness of the brooder. Smith (1980) points out that the "selfish" genes are the ones that will be represented in the next generation (i.e. a male which insures his genetic contribution to eggs he broods will increase his reproductive success). In nature, a male may not be certain which female of many he has mated with. Ridley (1978) described waterbugs as being monogynous, (i.e. a male carries the eggs of only one female). However, Kruse (unpubl. data) has shown that it is not unusual for males to have different size eggs at one time: these data indicate that multiple matings do occur. There is also no guarantee that a female has not mated with another male since copulating with him. Thus his best option appears to be repeated copulations before allowing any oviposition.

Smith (1979b) speculates that a male's ejaculate may

displace another male's sperm into the distal end of the spermatheca. Thus the previous male's sperm, still present, would continue to pose a threat to the current male's fitness. Numerous copulations would repeatedly flush a competitor's sperm back, reducing the threat of cuckoldry. Repeated copulations might also regularly replenish the current male's gametes in the optimal location for egg fertilization (Thornhill and Alcock, 1983).

Even these elaborate paternity-assurance efforts are not 100% effective: one male received two eggs from a female with whom he had never copulated. Another received five eggs from a female who had copulated with another male since copulating with him. However, these events are the exception, not the rule.

These copulation/oviposition bouts are under the male's control (Smith, 1979b). This is not surprising, since the female benefits regardless of which sperm are used in fertilization. In fact, females will resist a male's efforts to copulate again (pers. observ.); repeated copulations are costly to her in terms of both time and energy. Smith (1979a) reports the additional cost of the loss of eggs (up to five percent of a female's complement) due to interruption by male Abedus herberti forcing additional copulations. Apparently, the increased survival rate of offspring outweighs any costs incurred by either male or female behaviors in this system.

The first eggs were usually laid posteriorly on the male (108 of 114 oviposition bouts, 95%). (All exceptions were observed in trios. However, they did not appear to be the direct result of competition.) Each subsequent egg was laid adjacent to the others, working anteriorly and laterally. This appears to insure that the maximum number of eggs can be laid in the allotted space.

Within a few days after receiving a clutch, males appear reluctant to accept more eggs (Smith, 1979a; pers. observ.). Accepting new eggs might mean substantially increased brooding time and energy expenditure for a minimal evolutionary payoff. In obtaining as many eggs as possible in one mating sequence, the male can maximize the number of offspring and, at the same time, minimize brood time. Smith (1979a) reported that at the onset of the first oviposition bout, the male Abedus herberti extended his air straps, providing the female with a backstop against which she invariably deposited the first eggs. This behavior (although not directly observed in this study) may also exist in B. flumineum. This might explain why the first eggs are so often laid posteriorly, instead of moving posteriorly from the head.

In "two male:one female" matings in the laboratory (with access to females limiting male reproduction), both aspects of sexual selection were observed in male behavior, as predicted: intrasexual selection (i.e. physical aggression) was seen in males "striking" at each other.

Intersexual selection (i.e. "courtship competition") was seen in male pumping displays.

In "one male:two female" matings (with access to males limiting female reproduction), intrasexual selection (i.e. female-female competition) was seen in the form of a "pushing" behavior. However, no counterpart to the male's intersexual selection was observed (i.e. no female courtship was seen). At no time was an obvious female analog to male pumping observed (i.e. no female initiation of mating was seen). However, this does not eliminate the possibility of auditory or olfactory initiation. This "void" may be due to the fact that, even though access to males may be limiting to females (i.e. male backspace may be limiting), females may still make the larger parental investment. Thus what is observed may be "partial" sex-role reversal.

Smith (1980) has suggested that sexual roles in courtship may rely as much on circumstances of the moment as on sex-linked genetic programs. For instance, males do not appear to court as fervently when alone as they do when other males are present. This flexibility may be partly responsible for the varied behaviors observed under different conditions.

## Aspect II: Mating Preference

Smith (1979a) has suggested that female Abedus herberti prefer to mate with partially-encumbered males. He speculated that a small clutch of eggs may signal to the female a male's willingness to breed. It may also somehow indicate to the female that a male is a competent brooder. These ideas suggest "female preference" for a partially-encumbered male. However, it may be more a matter of "male dominance". An unencumbered male may compete for access to a female. However, he has no brooding costs. In contrast, a male with a partial clutch has already committed himself to fixed brooding costs (Smith, 1979a). It is to his advantage to maximize the number of eggs he broods. Thus a partially-encumbered male may simply out-compete an unencumbered male (i.e. a male with a small clutch may exhibit more pumps per minute than the other male, presumably attracting the female away from the unencumbered male.) This area of research warrants further attention.

In two instances (Table 6--male #243 with male #210 and male #169 with male #207) where both males became encumbered, the partially-encumbered males became fully encumbered. This suggests that the female may have fully-encumbered that male, at which point he would no longer accept eggs. The female then presumably began mating with the unencumbered male. In one instance (Table 6--male #183 with male #169), the partially-encumbered male became 90% encumbered, at which time he may have decreased his courting efforts.



As previously mentioned, a male should maximize the number of eggs he broods, due to potentially-high brood costs. This suggests that a male might prefer a heavily-gravid female over one which might give him only a partial clutch. Again, the question here is whether the male "prefers" a heavily-gravid female, or whether a heavily-gravid female simply "out-competes" a less-gravid female for male backspace.

My results (Tables 7, 8) suggest that the heavily-gravid female may have a breeding advantage over a less-gravid female: ten times of ten (100%), the heavily-gravid female bred with the male. In one case, the less-gravid female (who was remated) bred the following day, depositing 104 eggs (100% encumberment) on the male. Apparently she was capable of and ready to breed, yet was not allowed to: either the male discriminated against her, or she was out-competed by the more heavily-gravid female.

Results of this study suggest that males pump to attract females. Contingency table analysis (Table 2) indicates that males pump significantly more in the presence of other males than when alone. This appears to be intersexual selection. No female counterpart to male pumping was observed in female-biased situations. Results also suggest that heavily-gravid females may have a breeding advantage over less-gravid females.

This study suffers from extremely small sample sizes. This is partly due to my primary objective of completely

describing Belostoma flumineum courtship under a "one male:one female" sex ratio. Hopefully, this will serve as a useful pilot study for further investigation regarding the influence of proximate factors, such as varied sex ratios, on courtship behavior in species where the male exclusively cares for young.

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Figure 1. Copulatory positions of a female (left) and male (right) giant waterbug, Belostoma flumineum.



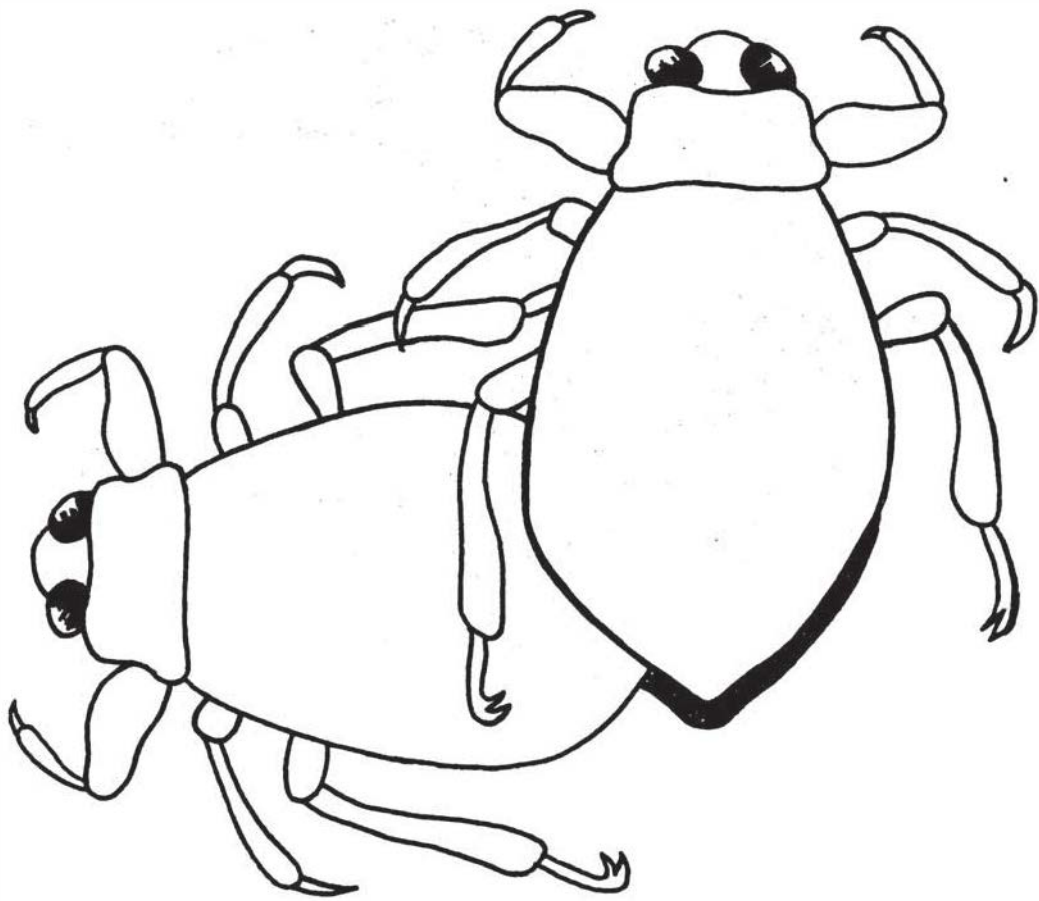


Figure 2. Oviposition positions of a female (left) and male (right) giant waterbug, Belostoma flumineum. Eggs are oviposited on the male's dorsum, working anteriorly.

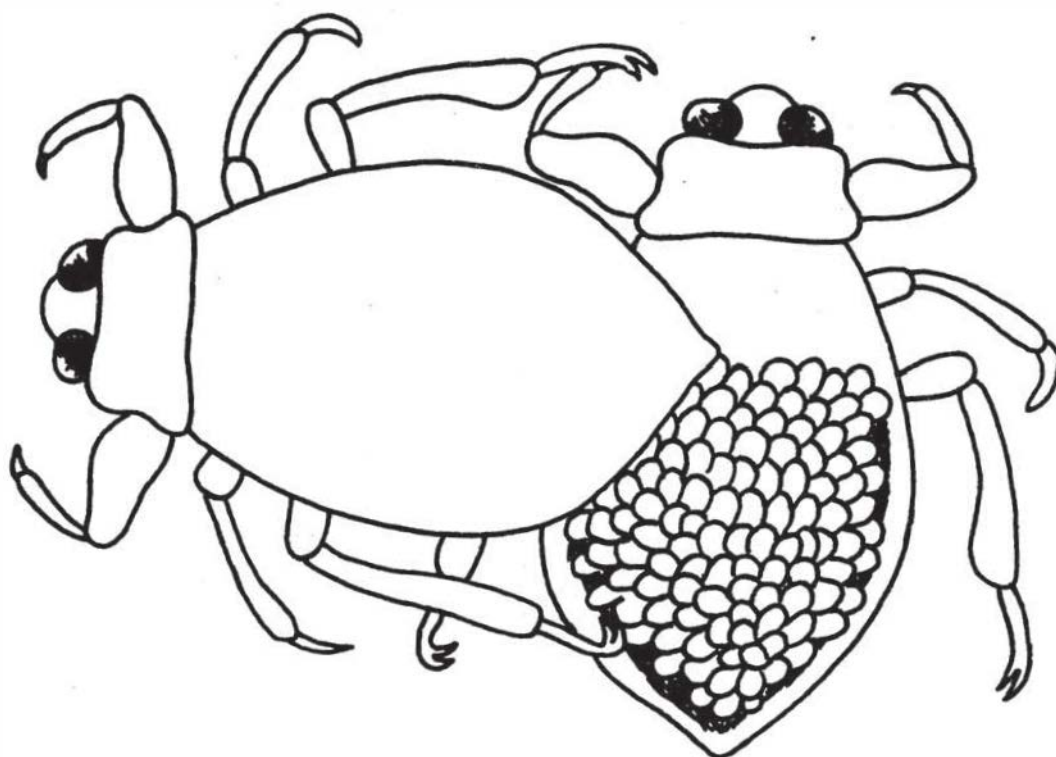


Figure 3. Sequence of events in mating of Belostoma flumineum in a "one male:one female" pairing.

# MATING BEHAVIOR

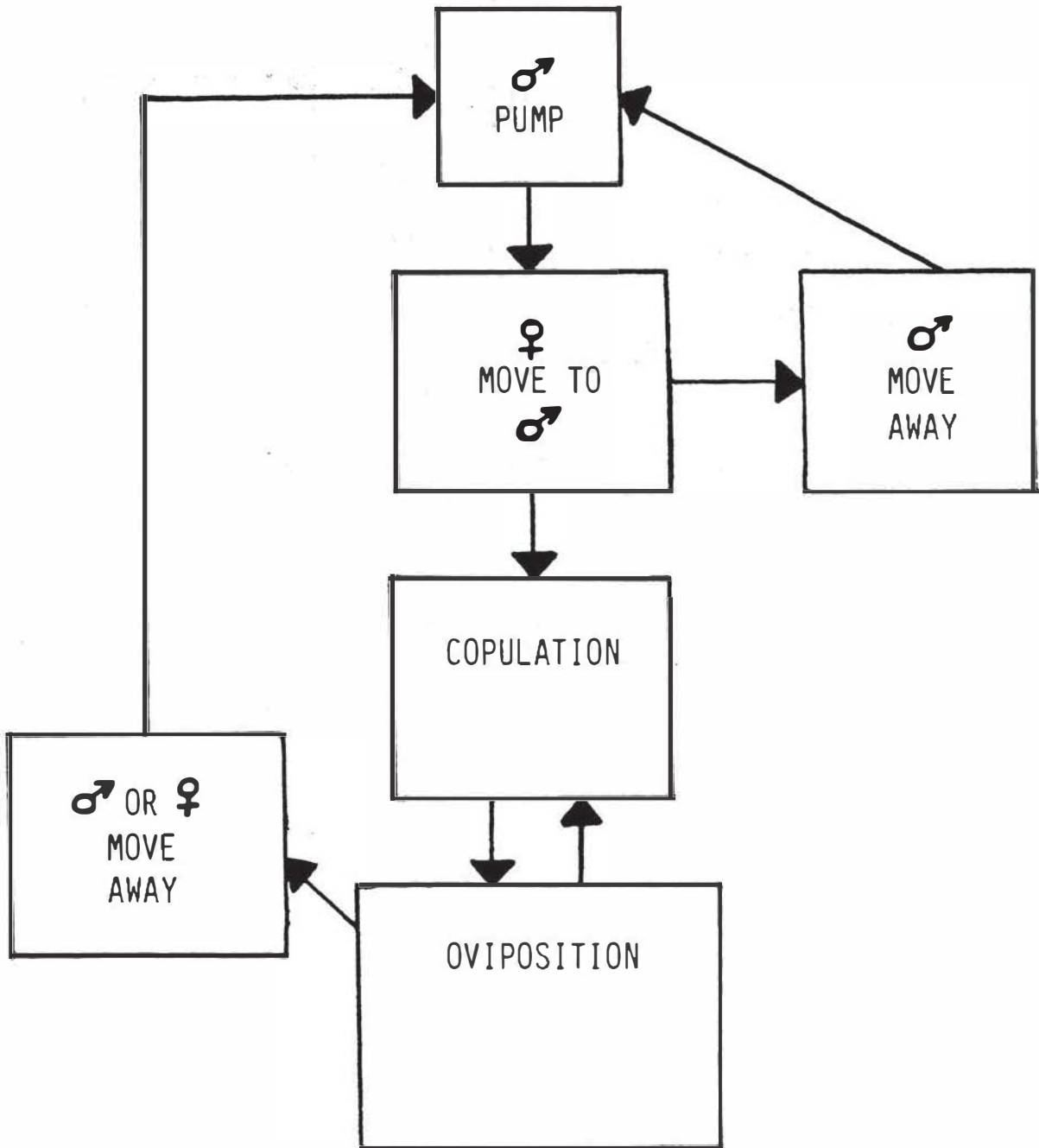


Figure 4. Sequence of events in mating of Belostoma flumineum in "two male:one female" and "one male:two female" trios. A indicates point of male pumping displays. B and C indicate points of female "pushing".

MATING BEHAVIOR

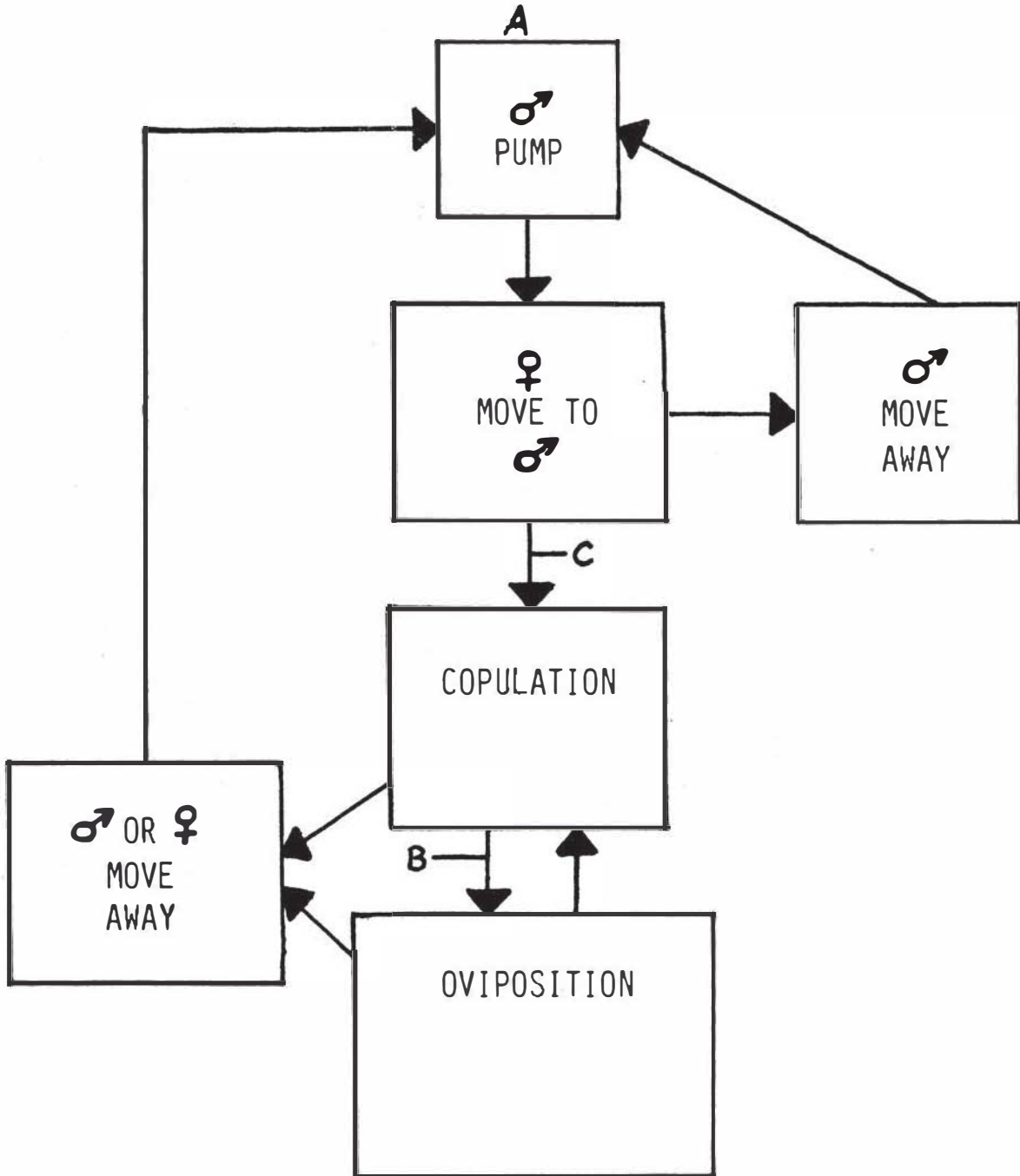


Table 1. Summary of data collected from matings.

Mating situation	Statistic	Number pumps per minute	Pumping sequence duration (seconds)	Copulation time (minutes)	Oviposition time (minutes)	Number eggs per oviposition bout
One male: one female	n*	19	19	49	144	51
	$\bar{X}$	15.5	190.5	2.7	1.0	3.9
	S	7.8	115.6	1.1	0.1	1.0
	Range	0.4- 28.0	26.0- 314.0	1.5- 5.8	0.7- 1.6	1- 5
Two males: one female	n*	59	59	35	95	25
	$\bar{X}$	28.1	62.7	2.7	0.9	4.1
	S	7.8	55.0	0.7	0.2	1.3
	Range	8.1- 40.0	11.0- 300.0	1.9- 4.2	0.6- 2.4	1- 6
One male: two females	n*	5	5	39	55	38
	$\bar{X}$	13.0	217.8	2.4	1.0	2.3
	S	9.0	127.8	0.9	0.3	1.2
	Range	4.7- 26.7	9.0- 300.0	1.0- 4.8	0.4- 1.8	1- 5

\* n = number of observations



Table 2. Contingency table analysis of male pumps per minute. Expected values are in parentheses.

Mating situation	Number pumps per minute			Total
	<14	15-24	>25	
One male: one female	11 (3.6)	4 (4.9)	4 (10.5)	19
Two males: one female	4 (11.4)	16 (15.1)	39 (32.5)	59
	15	20	43	78
$\chi^2 = 25.02, d.f.=2, p<0.001$				
One male: two females*	3	1	1	1

\* these data not included in analysis due to small sample size

Table 3. Data collected from two "one male:one female" pairings.

Mating number	Individual number	Statistic	Number pumps per minute	Pumping sequence duration (seconds)	Copulation time (minutes)	Oviposition time (minutes)	Number eggs per oviposition bout
1	43	n*	16	16	22	72	22
		$\bar{X}$	17.3	199.2	2.4	1.0	4.4
		S	6.9	111.9	1.0	0.1	0.7
		Range	8.4- 28.0	26.0- 300.0	1.5- 5.1	0.7- 1.6	3- 5
2	120	n*	3	3	27	72	29
		$\bar{X}$	5.9	144.0	3.0	1.0	3.6
		S	4.8	149.9	1.1	0.1	1.1
		Range	0.4- 9.3	31.0- 314.0	1.5- 5.8	0.8- 1.4	1- 5
		n*	19	19	49	144	51
		$\bar{X}$	15.5	190.5	2.7	1.0	3.9
		S	7.8	115.6	1.1	0.1	1.0
* n = number of observations							

Table 4. Data collected from four "two male:one female" trios.

Mating number	Individual number	Statistic	Number pumps per minute	Pumping sequence duration (seconds)	Copulation time (minutes)	Oviposition time (minutes)	Number eggs per oviposition bout
1	43	n*	10	10	4	5	2
		$\bar{X}$	24.4	105.2	2.6	0.9	2.5
		S	12.8	92.6	0.5	0.1	0.7
	44	Range	16.4-37.5	20.0-300.0	2.1-3.3	0.8-1.0	2-3
		n*	6	6	5	17	6
		$\bar{X}$	28.2	68.3	3.0	1.0	3.5
2	43	S	6.4	54.9	0.9	0.2	1.4
		Range	8.1-39.4	20.0-128.0	2.0-4.2	0.7-1.2	1-5
		n*	10	10	14	43	10
	44	$\bar{X}$	24.4	57.6	2.3	0.9	4.5
		S	7.2	38.8	0.4	0.2	1.4
		Range	16.2-35.9	12.0-135.0	1.9-3.3	0.6-1.4	1-6
3	44	n*	6	6	3	0	0
		$\bar{X}$	25.8	58.3	3.7	-	-
		S	6.4	32.5	0.4	-	-
	73	Range	13.1-35.0	12.0-98.0	3.4-4.2	-	-
		n*	12	12	2	0	0
		$\bar{X}$	33.0	52.9	3.8	-	-
4	38	S	6.6	50.0	0.6	-	-
		Range	19.2-39.6	11.0-187.0	3.4-4.2	-	-
		n*	15	15	1	3	1
	121	$\bar{X}$	28.7	51.8	2.6	1.2	4.0
		S	6.9	46.2	0	0.5	0
		Range	16.7-40.0	11.0-187.0	-	0.9-2.4	-
4	38	n*	0	0	6	27	6
		$\bar{X}$	-	-	2.6	0.9	4.7
		S	-	-	0.7	0.3	0.5
	121	Range	-	-	2.2-4.0	0.7-1.7	4-5
		n*	0	0	0	0	0
		$\bar{X}$	-	-	-	-	-
Total	S	-	-	-	-	-	
	Range	-	-	-	-	-	
	n*	59	59	35	95	25	
Total	$\bar{X}$	28.1	62.7	2.7	0.9	4.1	
	S	7.8	55.0	0.7	0.2	1.3	

\* n = number of observations

Table 5. Data collected from five "one male:two female" trios.

Mating number	Individual number	Statistic	Number pumps per minute	Pumping sequence duration (seconds)	Copulation time (minutes)	Oviposition time (minutes)	Number eggs per oviposition bout	
1	64	n*	4+	4+	8	18	8	
		$\bar{X}$	9.5	270.0	3.2	1.3	2.6	
		S	5.4	60.0	0.8	0.2	1.1	
		Range	4.7-	180.0-	1.8-	0.9-	1-	
			15.2	300.0	4.8	1.6	4	
		8	n*			5	4	6
	$\bar{X}$				3.0	1.2	2.3	
	S				1.1	0.1	1.2	
	Range				2.6-	1.1-	1-	
					4.6	1.1	4	
2	47	n*	1+	1+	9	7	5	
		$\bar{X}$	26.7	9.0	2.3	1.0	2.2	
		S	0	0	0.8	0.4	1.1	
		Range	-	-	1.0-	0.7-	1-	
					4.0	1.8	4	
		139	n*			3	5	3
	$\bar{X}$				2.0	0.9	1.3	
	S				0.3	0.4	0.6	
	Range				1.8-	0.6-	1-	
					2.4	1.7	2	
3	3	n*	0+	0+	7	6	6	
		$\bar{X}$	-	-	1.5	1.0	2.7	
		S	-	-	0.2	0.4	2.0	
		Range	-	-	1.4-	0.5-	1-	
					2.0	1.7	5	
		31	n*			2	3	2
	$\bar{X}$				1.6	0.6	1.5	
	S				0.2	0.2	0.7	
	Range				1.4-	0.4-	1-	
					2.0	0.7	2	
4	54	n*	0+	0+	3	5	3	
		$\bar{X}$	-	-	2.4	0.8	1.3	
		S	-	-	0.5	0.1	0.6	
		Range	-	-	2.0-	0.7-	1-	
					2.9	1.0	2	
		53	n*			0	0	0
	$\bar{X}$				-	-	-	
	S				-	-	-	
	Range				-	-	-	
5	9	n*	0+	0+	2	7	5	
		$\bar{X}$	-	-	2.0	0.8	2.6	
		S	-	-	0.0	0.1	1.1	
		Range	-	-	2.0-	0.7-	1-	
					2.0	1.0	4	
		31	n*			0	0	0
	$\bar{X}$				-	-	-	
	S				-	-	-	
	Range				-	-	-	
		n*	5	5	39	55	38	
		$\bar{X}$	13.0	217.8	2.4	1.0	2.3	
		S	9.0	127.8	0.9	0.3	1.2	

\* n = number of observations

+ data not divided with respect to individual females

Table 6. Oviposition on partially-encumbered vs. unencumbered males in "two male:one female" trios.

Male number	Initially encumbered	Clutch size	% encumberment	Newly-encumbered male	Clutch age when newly-encumbered (days)	Number new eggs	Total number eggs	Total percent encumberment	Partially-encumbered male bred	Unencumbered male bred	Both males bred	
110	+	52	50	*	1	104	156	100	*			
183	-	-	-	-	-	-	-	-				
114	+	55	50	*	1	83	138	100	*			
194	-	-	-	-	-	-	-	-				
110	+	65	50	*	1	51	116	80	*			
199	-	-	-	-	-	-	-	-				
169	+	52	50	*	1	81	81	90	*			
194	-	-	-	-	-	-	-	-				
169	+	26	30	*	2	56	56	50	*			
194	-	-	-	-	-	-	-	-				
114	+	47	50	*	1	26	73	70	*			
183	-	-	-	-	-	-	-	-				
110	+	68	50	-	5	-	68	50				
199	-	-	-	*	-	37	37	35		*		
199	+	37	35	-	1	-	-	-				
244	-	-	-	*	-	133	133	95		*		
244	+	68	50	*	1	53	121	90	*			
183	-	-	-	-	-	-	-	-				
165	+	60	50	-	1	-	60	50				
244	-	-	-	*	-	46	46	45		*		
243	+	66	50	*	2	11	77	55			*	
204	-	-	-	*	-	83	83	70				
183	+	54	50	*	2	34	88	90			*	
169	-	-	-	*	-	44	44	45				
243	+	59	55	*	2	42	101	90			*	
210	-	-	-	*	-	70	70	75				
68	+	41	60	*	1	92	133	100	*			
246	-	-	-	-	-	-	-	-				
114	+	43	40	-	1	-	43	40				
68	-	-	-	*	-	104	104	85		*		
169	+	44	45	*	1	57	101	95			*	
207	-	-	-	*	-	57	57	50				
207	+	15	10	*	1	13	28	25	*			
238	-	-	-	-	-	-	-	-				
									Total	9	4	4

+ denotes initial encumberment  
 \* denotes male which became encumbered  
 - denotes initial pad dropped

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Table 7. Encumberment by heavily-gravid vs. less-gravid females in "one male:two female" trios. After encumberment, both females were dissected.

Female number	Initial weight (grams)	Weight change (grams)	Breeding female	Number of eggs deposited on male	Number of eggs inside female	Total number eggs
172	0.385	-0.044	*	58	73	131
107	0.271	+0.006	-	-	39	39
162	0.380	-0.036	*	52	74	126
79	0.254	-0.004	-	-	23	23
156	0.362	-0.085	*	99	6	105
85	0.333	-0.008	-	-	33	33
168	0.384	-0.066	*	108	0	108
167	0.285	-0.004	-	-	32	32
163	0.376	-0.073	*	88	0	88
119	0.230	-0.004	-	-	38	38

\* denotes female which oviposited

Table 8. Encumberment by heavily-gravid vs. less-gravid females in "one male: two female" trios. After encumberment, the female which did not breed was remated.

Female number	Initial weight (grams)	Weight change (grams)	Breeding female	Number of eggs deposited on first male	Number days before second female bred	Number eggs deposited on second male
159	0.344	-0.059	*	68	-	-
160	0.309	+0.004	-	-	1	104
242	0.354	-0.051	*	73	-	-
305	0.275	-0.008	-	-	9	63
236	0.450	-0.093+	*	131	-	-
252	0.336	-0.000+	-	-	4	54
171	0.269	-0.034	*	94	-	-
170	0.234	-0.019	-	-	8	36
166	0.364	-0.042	*	49	-	-
164	0.320	-0.014	-	-	2	73

\* denotes female which oviposited  
 + weight loss over two days