

Multiple mating in a water strider: mutual benefits or intersexual conflict?

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Abstract. It has long been recognized that male and female interests in mating may be asymmetrical. The present study quantified experimentally several potential costs and benefits in mating multiply in female water striders, *Gerris odontogaster* (Zett.). Matings were costly to females, mainly in terms of increased predation risk and time/energy costs involved in carrying passive males. There were no balancing benefits to females in mating multiply. It is concluded that females should theoretically mate approximately every 10th day for maximal survival and fecundity and that multiple matings are not beneficial to females per se. However, females frequently mate several times every day. Several facts suggest that matings are enforced by males at the expense of females' primary interests and that an intersexual conflict over the mating decision exists. However, since a mating male repels copulatory attempts by other males, females may minimize costs by accepting superfluous matings in order to forage relatively undisturbed.

The primary function of copulation for males is to sire offspring, and males can generally increase their reproductive success by mating with many females (Darwin 1871; Bateman 1948; Trivers 1972). For females, the primary function of copulation is to fertilize their ova. If one mating provides females with sufficient sperm, and the males provide little but gametes in mating, there are no obvious reasons why females should benefit from further matings (Daly 1978; Parker 1979). Male and female interests in mating may thus be asymmetrical (e.g. Trivers 1972; Parker 1979, 1984).

Several potential costs to females may be involved in mating: (1) time and energy costs devoted to courtship and copulation; (2) increased risk of predation while mating; (3) risk of injury inflicted by the male; and (4) risk of disease or parasite transmission (see Daly 1978; Thornhill & Alcock 1983; Lewis 1987). Hence, one would predict that females should not mate many times (Thornhill & Alcock 1983). In some species, females become unreceptive or reluctant to mate after the first copulation (e.g. Linley & Adams 1972; Oh 1979; Gromko et al. 1984). However, despite the potential costs, females of many species mate several times during their lifespan (e.g. Thornhill & Alcock 1983; Eberhard 1985).

Several benefits may balance the costs experienced by females that mate multiply (see Walker 1980; Thornhill & Alcock 1983; Halliday & Arnold 1987). These adaptive explanations include: (1)

females replenish depleted sperm supplies; (2) females receive nutrients or other paternal investments from males; or (3) mating reduces risk of predation or mortality. Further, multiple mating may (4) be a hedge against sterility (or genetic defects) of the first mate, and may have genetical benefits, namely (5) increased genetic diversity of offspring and (6) superior genetic quality of the last mate.

Finally, females may mate multiply to avoid the costs of preventing matings, even if copulations are superfluous (e.g. Thornhill & Alcock 1983; Fincke 1984; Waage 1984; Wilcox 1984). In male-female encounters, males may frequently be under selection to re-mate whereas females may be under selection to resist matings. Such situations pose intersexual conflicts over the mating decision (Trivers 1972; Parker 1979). If males could evolve strategies or morphologies (Daly 1978; Thornhill 1980; Eberhard 1985; Hogg 1988) that made it costly for females to resist mating attempts, females could minimize costs by accepting matings without receiving balancing benefits in mating per se. Mating would then be a way of reducing male harassment (Walker 1980; Thornhill & Alcock 1983). However, empirical evaluations of the cost-benefit balance for females in repeated matings are scarce and hence desirable (Daly 1978; Walker 1980; Thornhill & Alcock 1983; Knowlton & Greenwell 1984; Eberhard 1985). In the present study, I assess the potential costs and benefits

associated with multiple mating in female water striders, *Gerris odontogaster* (Zett.). I also evaluate and discuss the results in relation to the theory of intersexual conflict (Trivers 1972; Parker 1979).

Mating Behaviour

Males and females of most water strider species (Heteroptera: Gerridae) exhibit multiple matings both in the laboratory and in the field (e.g. Vepsäläinen 1974; Wilcox 1984; Hayashi 1985; Wheelwright & Wilkinson 1985; Kaitala 1987; Arnqvist 1988). *G. odontogaster* males grasp females without prior courtship and attempt enforced copulations. Males possess an abdominal grasping apparatus which is essential for successful copulations. Females appear reluctant to mate; they try to dislodge males, primarily by a backward somersault behaviour. Dislodgement occurs in approximately 80–85% of the male mating attempts (Arnqvist, in press). *G. odontogaster* is a highly promiscuous species, mating regularly during the reproductive period. Females produce on average two or three eggs per day during a 1–2-month reproductive period (Vepsäläinen & Patama 1983). *G. odontogaster* as well as many other water strider species exhibit postcopulatory guarding of considerable duration, during which the male rides passively on the back of the female (e.g. Andersen 1982; Wilcox 1984; Vepsäläinen 1985; Arnqvist 1988).

GENERAL METHODS

The study population inhabited the Gimonäs pond, south-east of Umeå in northern Sweden (63° 48' N, 20° 19' E). For laboratory experiments, non-mated (immature) individuals were captured with a hand net on 5–6 May 1987. All laboratory experiments were conducted at $20 \pm 1^\circ\text{C}$. The illuminated period in the laboratory was adjusted every day, to correspond with the daylength in the field.

EGG VIABILITY AND EGG PRODUCTION

This experiment compared egg viability, egg production and female longevity between females kept with and without males in the laboratory.

Methods

The water striders were kept in plastic containers

measuring 30 cm in diameter, at a density of three per container. In the control group ($N=11$ containers), one female was kept constantly with two males. In the experimental group ($N=11$ containers), three females were kept in each container. Three randomly chosen males were introduced into each container in the experimental group on day 1 and removed on day 3. This procedure was repeated on day 30 (introduction of males) and day 33 (removal). Pieces of floating cork ($5.0 \times 5.0 \times 0.3$ cm) served as oviposition and resting sites. Egg batches were removed every third day for 48 days (until the first female died), and the total number of eggs was recorded. The viability of eggs was recorded after 6 days of isolation. Viable eggs were defined as those that contained embryos (see Andersen 1982). All water striders were fed daily with three *Drosophila* fruitflies. Feeding continued until all females in the control group had died.

Results

The egg viability of females isolated from males started to decrease approximately 10 days after isolation (Fig. 1). However, the proportion of viable eggs was not significantly lower than that of the control group until 18 days of isolation. When males were reintroduced to the isolated females for 3 days, the proportion of viable eggs increased rapidly to a level similar to that of the control group.

The decrease in viability of eggs of isolated females was accompanied by a decrease in egg production rate (Fig. 2). The egg production decreased gradually, but increased rapidly when males were reintroduced. There was no significant difference in mean egg production between the two groups until 12 days of isolation (in both isolation events; Fig. 2).

In the control group, where females were kept with males throughout the experiment, the overall frequency of viable eggs was 93% (totals). However, there was a slight but significant decrease in both viability ($r = -0.78$, $P < 0.01$; $Y = 101 - 0.32X$) and mean egg production ($r = -0.68$, $P < 0.01$; $Y = 12.6 - 0.13X$; t -test of $H_0: \beta = 0$, $P < 0.01$ in both cases) during the experiment.

After 69 days all females in the control group were dead, whereas 48% of the females in the experimental group were alive. The frequency of dead females was significantly higher in the control

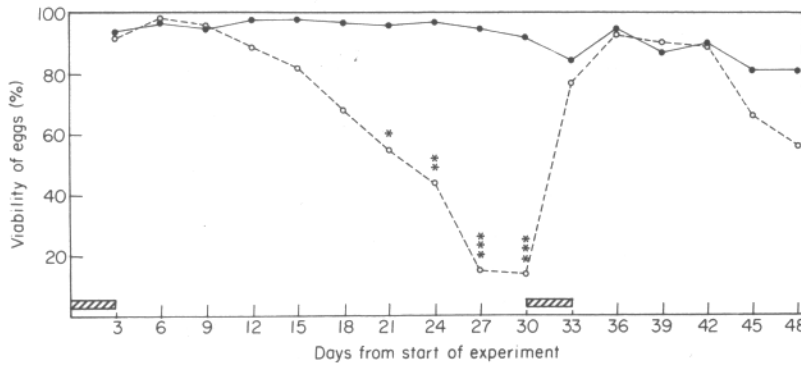


Figure 1. Temporal patterns of egg viability in females kept either constantly with males (●) or without males (○). Hatched bars indicate periods when the latter group of females had access to males. Chi-squared test; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

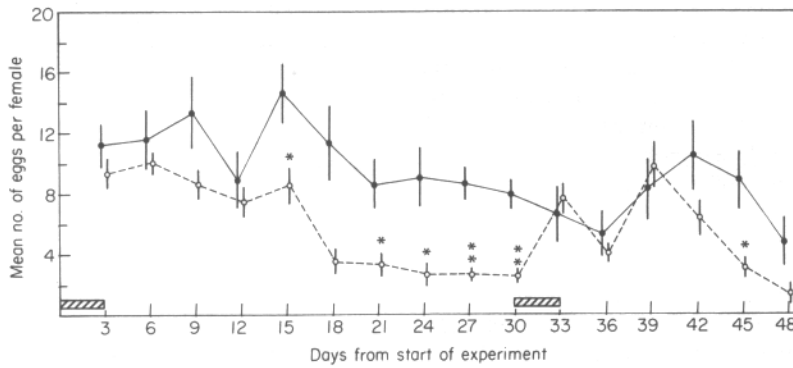


Figure 2. Mean (\pm SE) egg production per female per 3 days in females kept either constantly with males (●) or without males (○). Hatched bars indicate periods when the latter group of females had access to males. Mann-Whitney U -test; * $P < 0.05$; ** $P < 0.01$.

group ($\chi^2 = 8.38$, $P < 0.01$). Thus, females kept with males had a shorter lifespan than females kept without males.

GENETIC DIVERSITY OF OFFSPRING

This experiment compared growth and survival in the field of offspring of females mated with only one male and those of females mated with several males.

Methods

In the control group, each female ($N = 16$) was kept constantly with one male in a glass jar. The females in the experimental group ($N = 16$) were isolated individually in glass jars. Every second

day, these females were temporarily introduced for 8 h to 150 males in a plastic container (1.5×1.5 m) and were observed to mate at least once per female and occasion. The females in the experimental group thus mated with several males on several occasions. The water striders were fed daily with three frozen fruitflies each, and they were allowed to oviposit on floating pieces of cork in the jars.

After 8 days, the egg batches were removed and hatched. Five first instar larvae from each female were introduced into a floating enclosure, measuring 30 cm in diameter, in the field. The enclosures ($N = 32$), which were bounded only on the sides thus allowing food and predators to reach the sibling groups from above and below, were arranged in a 4×8 system flotilla. Sibling groups were distributed randomly within the flotilla. The

Table 1. Size and survival ($\bar{X} \pm \text{SD}$) in single- and multiple-paternity sibling groups

	Single-paternity sibling groups	Multiple-paternity sibling groups
No. of survivors per enclosure	1.12 \pm 1.20 (<i>N</i> = 16)	1.12 \pm 0.96 (<i>N</i> = 16)
Length of middle femora (second instar larvae; mm)	1.09 \pm 0.03 (<i>N</i> = 7)	1.07 \pm 0.02 (<i>N</i> = 4)
Length of middle femora (third instar larvae; mm)	1.68 \pm 0.05 (<i>N</i> = 11)	1.70 \pm 0.04 (<i>N</i> = 13)

sibling groups were isolated in the Gimonäs pond from 12 June to 4 July 1987 (22 days). At the end of the experiment, all surviving larvae were collected from the enclosures and preserved in 70% ethanol. In the laboratory all the larvae were classified according to larval instar, and the length of the middle femur was measured with a micrometer eyepiece. Hence, the experiment allowed comparisons of survival, development rate and size between the two categories of sibling groups.

Results

No significant difference either in survival or size was found between the single-paternity and multiple-paternity sibling groups (Table 1; Mann-Whitney *U*-test). Neither were there any significant differences between the categories in the frequency of occurrence of second and third instar larvae ($\chi^2 = 0.96$, ns). The overall mortality rate was 78% during the experiment.

PREDATION DURING MATING

To examine how mating affects predation risk, the vulnerability to an aquatic predator of females kept in pairs was compared with that of male-female pairs.

Methods

Adults of the backswimmer *Notonecta lutea* Müll. captured at the same site as the water striders were used as predators. Five backswimmers were starved for 3 days and placed individually in plastic aquaria measuring 30 cm in diameter. Each predator was presented to a water strider pair twice a day

for 8 successive days. The presentation order was reversed each day, so that the predators were first presented to a female-female pair and then to a male-female pair on days 1, 3, 5 and 7; the order was reversed on days 2, 4, 6 and 8. Each presentation lasted for 30 min, after which the outcome was recorded.

Results

The backswimmers seemed to detect the water striders by surface waves caused by movements (see also Lang 1980). When 'hanging' beneath the water surface, they adjusted their orientation in relation to the potential prey. A slow advancement towards the water strider was followed by a sudden attack. The backswimmers tried to grasp the water striders from below with their forelegs. When attacked, the water striders attempted to escape by making a sudden vertical leap followed by evasive skating.

In this experiment, predation occurred in 1.62 \pm 0.93 ($\bar{X} \pm \text{SD}$, *N* = 8) out of five aquaria when female-female pairs were exposed to the predators, whereas the corresponding figure for male-female pairs was 3.00 \pm 0.93 ($\bar{X} \pm \text{SD}$, *N* = 8). Hence, male-female pairs were more often subjected to predation than were female-female pairs (Mann-Whitney *U*-test, $P < 0.05$). Further, in male-female pairs, more females were taken as prey (75%) than were males ($\chi^2 = 6.0$, *N* = 24, $P < 0.05$). In no case did the predator take more than one individual as prey during one presentation. Converted to probabilities, a particular female in a male-female pair thus had almost three times as high a probability of being captured by the predator in this experiment, as had each particular female in female-female pairs $((0.75 \times 3.00)/5 = 0.45$ versus $(0.5 \times 1.62)/5 = 0.16$).

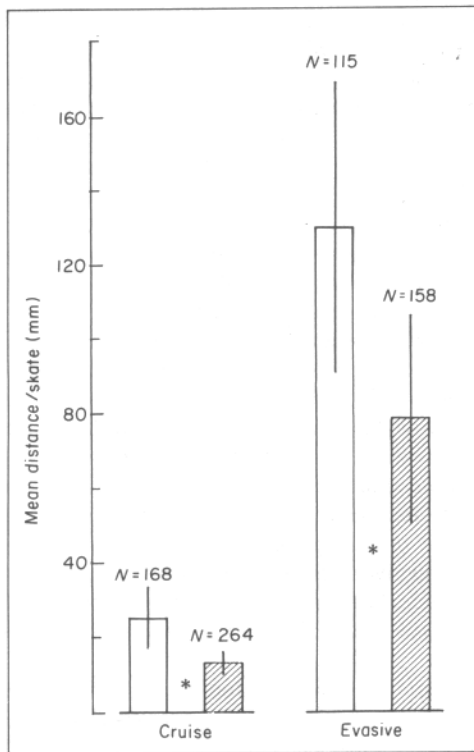


Figure 3. Mean mobility (\pm SD) of single females and females in copula during cruise and evasive skating. □ single females; ■ females in copula. *t*-test, * $P < 0.001$.

MOBILITY

This experiment compared the mobility of single females and mating females.

Methods

Water striders were recorded with a videotape recorder in a plastic container measuring 1.0 x 1.5 m. Two types of skating movement were recorded: undisturbed cruise skating and evasive skating. Evasive skating was induced by dropping a piece of Styrofoam into the margin of the container. The mobility was subsequently measured on a monitor in slow motion replays, and scaled to actual distance. Mobility was defined as the distance covered in each skate.

Results

The mobility of mating females was reduced to approximately 50–60% of that of single females

during both cruise and evasive skating (Fig. 3). The lower mobility of mating females was highly significant in both types of skating (*t*-test, $P < 0.001$ in both cases).

DISCUSSION

Potential Benefits to Females

Females were able to store viable sperm without any decrease in fertilization efficiency for approximately 10 days. By contrast, in *G. thoracicus* and *G. lateralis* longevity of sperm is approximately 14 and 30 days, respectively (Kaitala 1987; Arnqvist 1988). Thus, *G. odontogaster* females do not need to mate more often than approximately every 10th day in order to receive sufficient viable sperm to fertilize their eggs.

Males of some insect species transfer nutritional resources to females with their ejaculates. This type of paternal investment may be beneficial to females, e.g. in terms of increased fecundity or survival (see Thornhill & Alcock 1983 for a review). In the present study, the egg production of females kept without males was not significantly lower than that of females kept with males until 12 days of isolation. The subsequent reduction in the rate of egg production could be a result of lack of essential or beneficial ejaculate substances (e.g. nutrients). However, since the decrease in egg production was accompanied by a decrease in fertilization rates, the lower egg production exhibited by females after a period of isolation could also be interpreted as a compensating decrease in egg production rate due to lack of viable sperm. It is thus difficult to distinguish the proximate factor causing the decrease in egg production of isolated females (lack of ejaculate substances or lack of viable sperm). Nevertheless, since the egg production of isolated females did not differ significantly from the control group until 12 days of isolation, *G. odontogaster* females should not need to mate more often than approximately every 10th day in order to produce eggs at a normal rate. Any paternal investment that may occur thus seems to be of minor importance to females. Similar temporal patterns of egg production, egg viability and female longevity have also been observed in isolated *G. thoracicus* females (Kaitala 1987).

Walker (1980) proposed that mating may benefit females by reducing the risk of predation. However, this was clearly not the case in *G. odontogaster*

(see below). Walker (1980) also suggested that the male may serve as a decoy during mating, allowing the female to escape predation. In *G. odontogaster*, however, females were more vulnerable to predation. It is worth noting that backswimmers are considered one of the main predators of water striders (e.g. Spence 1986), and that *Notonecta* species are widely distributed and abundant aquatic predators.

The advantage of a genetically diverse set of offspring has been considered important for the evolution of sexual reproduction and recombination (see Stearns 1987 for a recent review). Multiple mating by females may actually represent a female strategy to increase further the diversity of her offspring (Pease 1968; Walker 1980). Compared with recombination itself, however, mating with more than one male has been ascribed a very slight contribution to the genetic diversity of sexually produced offspring (Williams 1975). The issue is still controversial (e.g. Knowlton & Greenwell 1984; Parker 1984). In the present study, when offspring were subjected to different potential selective mechanisms under semi-natural conditions (e.g. sibling competition, predation, temperature variations), I did not find any significant differences in growth or survival between single- and multiple-paternity sibling groups. This indicates that mating multiply in order to produce a genetically more diverse set of offspring may not be a major female benefit.

Potential Costs to Females

The most universal costs to females of mating may be time and energy costs (Thornhill & Alcock 1983). In *G. odontogaster*, females are most likely to have a higher energetic skating expenditure when carrying a passive male. Such costs are indicated by the lower mobility of females in copula in the present study. The reduction in mobility during cruise skating can also be expressed as time/energy costs in terms of a decreased foraging efficiency, since water striders use a searching foraging strategy (Andersen 1982).

An often cited cost of mating is an increased vulnerability to predators (Daly 1978; Thornhill & Alcock 1983; Lewis 1987). However, only one study has given empirical evidence that female insects (a beetle, *Photinus collustrans*) experience an increased risk of predation during mating (Wing 1988; see also Thornhill & Alcock 1983). Female

Gerris odontogaster in this study were also more vulnerable to predators when mating. Though the exact mechanisms were not specified, male-female interactions obviously increased the predation risk. Several factors may be important, namely an increased conspicuousness to predators, reduced attention and reduced mobility (i.e. ability to escape) during mating. These factors are not mutually exclusive, and they probably all contribute to increasing the vulnerability to predators during both copulation and guarding.

In water striders, precopulatory male-female interactions often involve aggressive elements (Spence 1979; Wilcox 1979, 1984; Hayashi 1985; Wheelwright & Wilkinson 1985; Arnqvist 1988) during which females may be injured or killed. As mentioned earlier, females kept without males lived longer than females kept with males. Though this should be interpreted primarily as a result of reproductive stress due to a higher oviposition rate in females kept with males, it may also be due to an increased risk of, for example, injury during mating.

A number of both endoparasites and ectoparasites are present in many different species of water striders (Andersen 1982; Tieszen et al. 1983). Though it has not been demonstrated, some of these parasites (e.g. mites) may be transferred during mating.

Evaluation of Female Costs and Benefits

As seen above, mating in *G. odontogaster* involves several costs for females. Males most probably benefit from multiple matings by increasing reproductive success (cf. Arnqvist 1988). This study failed to demonstrate any benefits to females in mating more often than approximately every 10th day. Despite this, multiple mating may involve minor benefits that I could not detect, or did not test. However, it seems unlikely that such benefits would counterbalance the quite severe costs to females in mating multiply. According to this study, females of *G. odontogaster* should thus theoretically mate only approximately every 10th day for maximal survival and fecundity. In reality, females both in the laboratory and in the field mate more often, frequently several times every day (e.g. Vepsäläinen 1974). However, the mating behaviour of *G. odontogaster* suggests that copulations are enforced by males at the expense of the primary interests of females.

The existence and resolution of evolutionary conflicts of interest between the sexes is controversial (e.g. Parker 1984; Eberhard 1985). Nevertheless, several facts suggest that such a basic conflict exists in *G. odontogaster*: females mate more frequently than would seem adaptive; females are reluctant and copulations are enforced by males; and males are provided with an 'anti-reluctance' grasping apparatus (Arnqvist, in press). Male water striders also have genital claspers, the functional significance of which is obscure (Andersen 1982). These claspers may be the result of an evolutionary race of male and female genitalia (but see Eberhard 1985 for a further discussion). The fact that the mating behaviour and mating patterns of several other water strider species resemble those of *G. odontogaster* (e.g. Spence 1979; Wilcox 1979; Wheelwright & Wilkinson 1985; Arnqvist 1988) suggests that this species is not in any way extreme and that intersexual conflicts may occur in several other species as well.

The postcopulatory guarding phase in water strider matings has been considered beneficial to both males (Arnqvist 1988) and females (Wilcox 1984). Wilcox (1984) reported that females of *G. remigis* forage effectively only while carrying a passive male on their backs. A copulating or guarding male repelled copulatory attempts by other males. This is true for *G. odontogaster* as well. However, to females, costs are involved in carrying passive males and multiple copulations are not beneficial per se. The best possible female option should thus be to escape effectively or repel 'court-ing' males, and so avoid superfluous matings. If this is not possible, females may simply be making the best of a bad situation. Females may thus minimize costs by accepting costly and superfluous copulations and guardings in order to forage without being harassed and disturbed by other males.

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REFERENCES

- Andersen, N. M. 1982. *The Semiaquatic Bugs (Hemiptera, Gerromorpha): Phylogeny, Adaptations, Biogeography and Classification*. Klampenborg: Scandinavian Science Press.
- Arnqvist, G. 1988. Mate guarding and sperm displacement in the water strider *Gerris lateralis* Schumm. (Heteroptera: Gerridae). *Freshwat. Biol.*, **19**, 269–274.
- Arnqvist, G. In press. Sexual selection in a water strider: the function, mechanism of selection and heritability of a male grasping apparatus. *Oikos*.
- Bateman, A. J. 1948. Intra-sexual selection in *Drosophila*. *Heredity*, **2**, 349–368.
- Daly, M. 1978. The cost of mating. *Am. Nat.*, **112**, 771–774.
- Darwin, C. 1871. *The Descent of Man and Selection in Relation to Sex*. London: John Murray.
- Eberhard, W. G. 1985. *Sexual Selection and Animal Genitalia*. Cambridge, Massachusetts: Harvard University Press.
- Fincke, O. M. 1984. Sperm competition in the damselfly *Enallagma hageni* Walsh (Odonata: Coenagrionidae): benefits of multiple mating to males and females. *Behav. Ecol. Sociobiol.*, **14**, 235–240.
- Gromko, M. H., Newport, M. E. A. & Kortier, M. G. 1984. Sperm dependence of female receptivity to remating in *Drosophila melanogaster*. *Evolution*, **38**, 1273–1282.
- Halliday, T. & Arnold, S. J. 1987. Multiple mating by females: a perspective from quantitative genetics. *Anim. Behav.*, **35**, 939–941.
- Hayashi, K. 1985. Alternative mating strategies in the water strider *Gerris elongatus* (Heteroptera, Gerridae). *Behav. Ecol. Sociobiol.*, **16**, 301–306.
- Hogg, J. T. 1988. Copulatory tactics in relation to sperm competition in Rocky Mountain bighorn sheep. *Behav. Ecol. Sociobiol.*, **22**, 49–59.
- Kaitala, A. 1987. Dynamic life-history strategy of the waterstrider *Gerris thoracicus* as an adaptation to food and habitat variation. *Oikos*, **48**, 125–131.
- Knowlton, N. & Greenwell, S. R. 1984. Male sperm competition avoidance mechanisms: the influence of female interests. In: *Sperm Competition and the Evolution of Animal Mating Systems* (Ed. by R. L. Smith), pp. 61–84. London: Academic Press.
- Lang, H. H. 1980. Surface wave discrimination between prey and nonprey by the backswimmer *Notonecta glauca* L. (Hemiptera, Heteroptera). *Behav. Ecol. Sociobiol.*, **6**, 233–246.
- Lewis, W. M., Jr. 1987. The cost of sex. In: *The Evolution of Sex and its Consequences* (Ed. by S. C. Stearns), pp. 33–57. Basel: Birkhäuser Verlag.
- Linley, J. R. & Adams, G. M. 1972. A study of the mating behaviour of *Culicoides mellus* (Coquillett) (Diptera: Ceratopogonidae). *Trans. R. entomol. Soc. Lond.*, **124**, 81–121.
- Oh, R. J. 1979. Repeated copulation in the brown planthopper, *Nilaparvata lugens* Stål (Homoptera; Delphacidae). *Ecol. Entomol.*, **4**, 345–353.
- Parker, G. A. 1979. Sexual selection and sexual conflict. In: *Sexual Selection and Reproductive Competition in Insects* (Ed. by M. S. Blum & N.A. Blum), pp. 123–166. New York: Academic Press.

- Parker, G. A. 1984. Sperm competition and the evolution of animal mating strategies. In: *Sperm Competition and the Evolution of Animal Mating Systems* (Ed. by R. L. Smith), pp. 1–60. London: Academic Press.
- Pease, R. W. 1968. The evolution and biological significance of multiple pairing in Lepidoptera. *J. Lepid. Soc.*, **22**, 197–209.
- Spence, J. R. 1979. Microhabitat selection and regional coexistence in water-striders (Heteroptera: Gerridae). D.Phil. thesis, University of British Columbia.
- Spence, J. R. 1986. Relative impacts of mortality factors in field populations of the waterstrider *Gerris buenoi* Kirkaldy (Heteroptera: Gerridae). *Oecologia (Berl.)*, **70**, 68–76.
- Stearns, S. C. (Ed.) 1987. *The Evolution of Sex and its Consequences*. Basel: Birkhäuser Verlag.
- Tieszen, K., Heywood, P. & Molyneux, D. H. 1983. Ultrastructure and host-parasite association of *Blasotrichidia gerridis* in the ventriculus of *Gerris odontogaster* (Gerridae: Hemiptera). *Can. J. Zool.*, **61**, 1900–1909.
- Thornhill, R. 1980. Rape in *Panorpa* scorpionflies and a general rape hypothesis. *Anim. Behav.*, **28**, 52–59.
- Thornhill, R. & Alcock, J. 1983. *The Evolution of Insect Mating Systems*. Cambridge, Massachusetts: Harvard University Press.
- Trivers, R. L. 1972. Parental Investment and Sexual Selection. In: *Sexual Selection and the Descent of Man* (Ed. by B. Campbell), pp. 136–179. London: Heinemann.
- Vepsäläinen, K. 1974. Determination of wing length and diapause in water-striders (*Gerris* Fabr., Heteroptera). *Hereditas*, **77**, 163–176.
- Vepsäläinen, K. 1985. Exclusive female vs. male territoriality in waterstrider (Gerridae) species: hypothesis of function. *Ann. Entomol. Fenn.*, **51**, 45–49.
- Vepsäläinen, K. & Patama, T. 1983. Allocation of reproductive energy in relation to the pattern of environment in five *Gerris* species. In: *Diapause and Life Cycle Strategies in Insects* (Ed. by V. K. Brown & I. Hodek), pp. 189–207. The Hague: Dr W. Junk.
- Waage, J. K. 1984. Sperm competition and the evolution of odonate mating systems. In: *Sperm Competition and the Evolution of Animal Mating Systems* (Ed. by R. L. Smith), pp. 251–290. London: Academic Press.
- Walker, W. F. 1980. Sperm utilization strategies in nonsocial insects. *Am. Nat.*, **115**, 780–799.
- Wheelwright, N. T. & Wilkinson, G. S. 1985. Space use by a neotropical water strider (Hemiptera: Gerridae): sex and age-class differences. *Biotropica*, **17**, 165–169.
- Wilcox, R. S. 1979. Sex discrimination in *Gerris remigis*: role of a surface wave signal. *Science, N.Y.*, **206**, 1325–1327.
- Wilcox, R. S. 1984. Male copulatory guarding enhances female foraging in a water strider. *Behav. Ecol. Sociobiol.*, **15**, 171–174.
- Williams, G. C. 1975. *Sex and Evolution*. Princeton, New Jersey: Princeton University Press.
- Wing, S. R. 1988. Cost of mating for female insects: risk of predation in *Photinus collustrans* (Coleoptera: Lampyridae). *Am. Nat.*, **131**, 139–142.

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