

SEXUAL DIMORPHISM AND BEHAVIOUR IN THE WATER STRIDER *GERRIS CHILENSIS* (BERG) (HEMIPTERA: GERRIDAE)

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ABSTRACT

Gerris chilensis (Berg) is a semiaquatic insect that lives on ponds next to rivers, showing sexual size dimorphism biased to females. The objective of this study was to compare the morphology and behaviour of males and females in the context of differential reproduction investment. Multivariate analysis showed significant differences in weight, abdomen length and width, thorax length, and width of the head. A positive relationship was found between female abdomen size and fecundity (number of eggs). To assess behavioural differences between sexes, four behavioural events were defined (aggression, grabbing, interference and coupling), and experiments set up in which sexual ratios were manipulated. Since nymphs do not display sexual behaviour, they were used as control. Grabbing and interference was higher in males, and did not appear in nymphs and females treatments, suggesting that males invest comparatively more than females in mate searching behaviour. Aggression was found in all groups, but it was higher in the only-nymph and only-female treatments, suggesting that these insects behave as food constrained organisms. These results are discussed in terms of hypotheses concerning evolution of sexual dimorphism.

Key words: sexual dimorphism, behaviour, body size, fecundity, *Gerris chilensis*.

RESUMEN

Gerris chilensis (Berg) is a semiaquatic insect that lives on ponds next to rivers, showing sexual size dimorphism biased to females. The objective of this study was to compare the morphology and behaviour of males and femaleS in the context of differential reproduction investment. Multivariate analysis showed significant differences in weight, abdomen length and width, thorax length, and width of the head. A positive relationship was found between female abdomen size and fecundity (number of eggs). To assess behavioural differences between sexes, four behavioural events were defined (aggression, grabbing, interference and coupling), and experiments set up in which sexual ratios were manipulated. Since nymphs do not display sexual behaviour, they were used as control. Grabbing and interference was higher in males, and did not appear in nymphs and females treatments, suggesting that males invest comparatively more than females in mate searching behaviour. Aggression was found in all groups, but it was higher in the only-nymph and only-female treatments, suggesting that these insects' behave as food constrained organisms. These results are discussed in terms of hypotheses concerning evolution of sexual dimorphism.

Keywords: sexual dimorphism, behaviour, body size, fecundity, *Gerris chilensis*

INTRODUCTION

One of the most commonly seen phenomena in animals is sexual dimorphism, particularly size

differences. The evolution of these differences reflects the net effect of selection and constraints acting on both sexes (Fairbairn & Preziosi, 1996; Preziosi & Fairbairn, 2000), including phylogeny (Andersen, 1994), allometric relationships (Fairbairn & Preziosi, 1994) and genetic covariance matrix (Lande, 1980). The maintenance of dimorphism has been shown to be highly related to the specific roles of males and females particularly in relation to differential energy investment. Greater

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body size in females is associated with egg production (Darwin, 1874; Preziosi & Fairbairn, 1996), which usually implies a higher cost than sperm production (Greenwood & Adams, 1987). Thus, females in contradistinction to males, direct their energy budget more to food acquisition than to mate finding (Darwin, 1874; Blanckernhorn *et al.*, 1995).

The first objective of this work is to study sexual dimorphic traits of *G. chilensis* and to look for possible relationships between these differences and the specific reproductive roles of both sexes. Secondly, to test the expectation of finding differences between sexes in mating searching behaviour, with the sex performing the least offspring investment making the highest effort in mate finding behaviour.

NATURAL HISTORY

The water strider, *Gerris chilensis* (Berg) is an hemipteran semi-aquatic predator and scavenger (Berg, 1881; Reed 1901), which lives on the surface of ponds next to water sources, feeding on floating dead organism. Reed (1901) described the *G. chilensis* as a rugged dark brown, with grey spots on the abdomen, covered with pale short hair. Usually, they shown an orange line in the pronotum anterior half. Both sexes show forms which exhibit elongated pronotum, covering the base of the elytra. Legs are thin and long and of the same colour as the body; forelegs are short and robust, and claws are present close to the tip of the last tarsal segment (Porter, 1924; Bachmann, 1966). Adults have five antennal segments, Antennal segment 1 approximately equal or longer than 2 plus 3, III tibia longer four times than tarsi 1. (Berg, 1881). The striders have been seen in the field feeding on lepidoptera (Heterocera), diptera (Tipulidae, Culicidae), orthoptera (Gryllidae), blattaria, hymenoptera (Sphecidae, Vespidae, Megachilidae, Formicidae) and also small batracia (personal observations).

The genus *Gerris* has a characteristic way of mating (Fairbairn, 1993; Rowe & Arqnvist, 1996): the male catches the female with the first pair of legs and climbs on her back, both swimming coupled for a while (Weigensberg & Fairbairn, 1996). A common trait to distinguish sexes is body size, females being larger than males or juveniles. The genus also display food-based territorial

behaviour and is resource restricted (Blanckerhorn & Perner, 1994; Blanckerhorn, 1991; Huerta, unpublished).

MATERIALS AND METHODS

This study was carried out in the Río Clarillo National Reserve (35° 51' S, 70° 29' W), 45 km Southeast of Santiago, Chile, between December 2000 and February 2001.

The density of striders was calculated as the ratio between the number of insects (regardless of their developmental stage) and the pond area. The sex ratio was determined from collections of individuals in six different ponds at two different places, using the same capture effort in both cases (five net captures per pond). Living individuals of both sexes were collected, and brought to the laboratory for morphological measurements. They were maintained in artificial ponds (50 x 50 x 10 cm, length x width x water depth) and fed with dead flies, bees and wasps.

Morphological measurements: Recently dead flatted individuals were photographed with a colour high-resolution digital camera (Sony Mavica FD95) and their morphological measurements (Figure 1) determined with SigmaScan ® digital measuring software. Differences in total length between sexes were compared with a Mann-Whitney U test (Zar, 1996), and the total length-standardised morphological measurements were compared using discriminant function analysis.

Females and males were weighed both fresh and dried, and body weight differences were assessed by ANOVA followed by Tukey test. A group of females (n=20) was dissected, and the eggs inside abdomen counted and measured. The relationship between number of eggs and female traits was studied using linear regression analysis.

Behavioural study: The behavioural observations were performed in the field, next to the natural ponds, using plastic bowls as artificial ponds (42 x 28 x 8 cm, length x width x water depth). The number of insects in each bowl (four adults) was defined based on the natural density determined

Four different behavioural patterns for *G. chilensis* were distinguished: i) Aggression: when one individual hits another with the legs (Fig. 2A). ii) Grabbing: when one individual holds another by

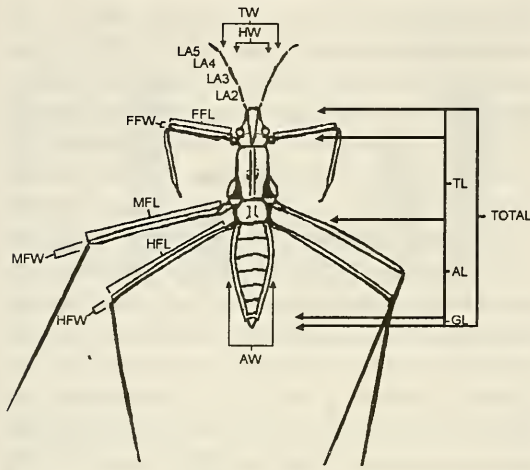


Figure 1. Ventral view of a female *Gerris chilensis* with morphological measurements indicated. Total body length (TOTAL) was employed to standardise other measurements: the length (AL) and width (AW) of abdomen and thorax (TL and TW, respectively). Head width (HW), length and width of the three femurs (FFL, FFW, MFL, MFW, HFL and HFW), four of the five antennal segments lengths (from second to fifth segments) were also measured (LA2, LA3, LA4 and LA5).

the thorax with the first pair of legs, behaviour commonly seen in males (Fig. 2B). iii) Coupling: when a male holds a female for a long time and they swim together, a behaviour exclusive for the female-male interactions (Fig. 2C). iv) Interference: when a non-paired insect joins an existing pair (Fig. 2D). In order to assess the general behaviour patterns of *G. chilensis* under different sex ratios, a treatment with only nymphs (N), used as control to sexual behaviours due to that they do not display sexual behaviours, and five treatments with different numbers of females (F) and males (M), were set up as follows: i) 4N; ii) 0F/4M; iii) 1F/3M; iv) 2F/2M; v) 3F/1M and vi) 4F/0M. Each observation lasted five minutes and started after one minute of acclimatisation.

Since the behavioural patterns defined occurred very fast inside the bowls, three persons made simultaneous observations and later an average of the three observations was determined. To avoid pseudoreplication, the insects employed were always changed between treatments. Also the water

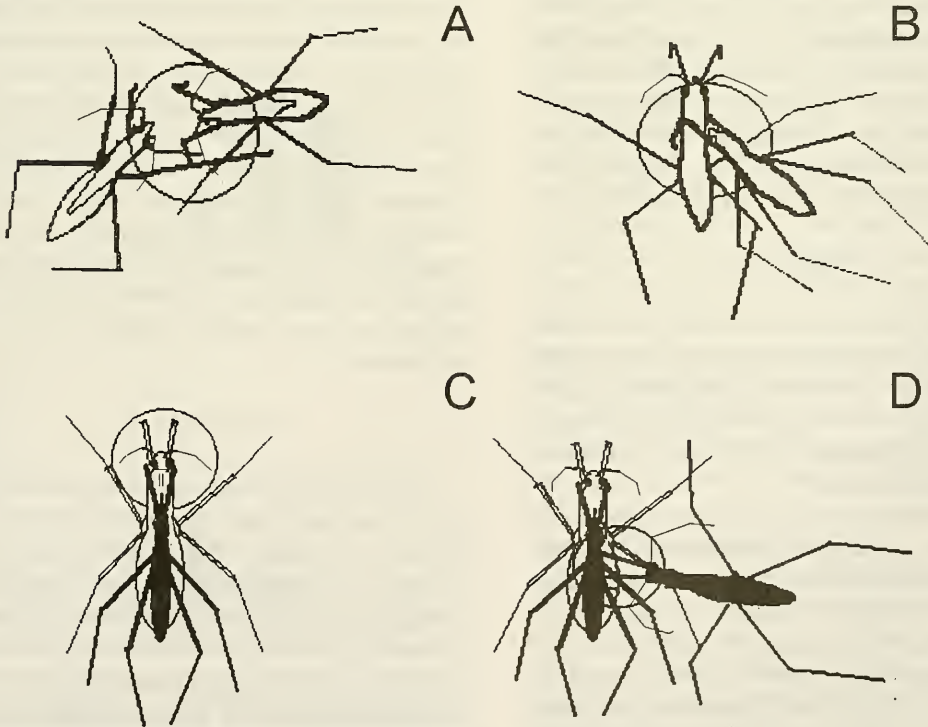


Figure 2. Behavioural patterns exhibited by *G. chilensis*: A) Aggression is a typical attacking behaviour between conspecifics, in which one insect comes next to another and kicks it. B) In the grabbing behaviour, one water strider holds another by the thorax with its first pair of legs. C) Coupling occurs when a male holds a female by the thorax and after that the pair swims together for a long time. D) Interference behaviour occurs when a water strider joins an existing male-female pair and tries to separate it.

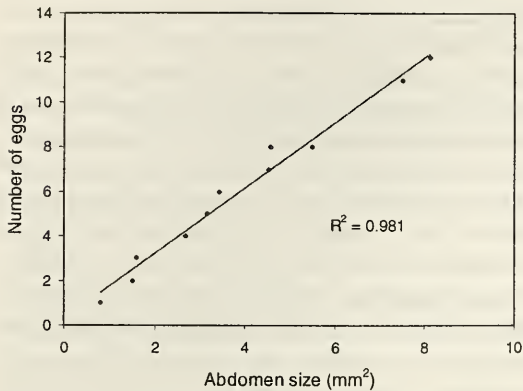


Figure 3. Relationship between fecundity and abdomen size. The ordinates indicate fecundity in terms of number of eggs per abdomen and the abscises indicate abdomen size (calculated as the product of abdomen length and width).

of the bowl was always changed. Sixteen replicates of each treatment were performed.

The number of behavioural events of any given type was divided by the total number of behavioural events displayed in each treatment in order to standardise the results for the total activity of the experimental individuals. Since data were not normally distributed, Kruskal-Wallis non-parametric test was performed followed by a posteriori multiple comparisons test (Siegel & Castellan, 1988) to know if the frequency of behaviours changed between the different sex ratios.

RESULTS

The density of striders at the study site was 40 adults (range: 2-130) and 67 nymphs (4-136) per square meter ($n = 10$). The sex proportion of adults was determined over the total number of individuals captured ($n = 96$ females, $n = 126$ males, sex ratio = 1.3125 males/females).

The difference in body length was significant between sexes, females being larger than males ($U = 92$ $p < 0.01$, Mann-Whitney U test). A discriminant function analysis showed a significant discrimination between males and females by morphological traits (Wilks' Lambda: 0.012; $F(16,23) = 114.29$ $p < 0.001$). Abdomen was larger and wider in females than in males, while thorax was larger and head was wider in males than in females (Table 1).

Significant differences were found between sexes

in weights and between fresh and dry weight measurements (two way ANOVA, $p < 0.001$). Thus, female fresh weight (0.0415 ± 0.0012 g, mean \pm standard error) was higher than male fresh weight (0.0223 ± 0.0004 g) and female dry weight (0.0137 ± 0.0006 g) was also higher than male dry weight (0.008 ± 0.0008 g) (Tukey HSD test; $p < 0.001$). The differences between fresh and dry weight for each sex were also significant ($p < 0.001$ for both females and males). Gravid and non-gravid females differed in water content, fresh minus dry weight, (gravid = 0.0472 ± 0.0008 g, $n = 11$; non-gravid = 0.033 ± 0.0005 g, $n = 9$); (student test for independent variables; $p = 0.0006$). The relationship between number of eggs and size of abdomen (Figure 3) was positive and significant ($p < 0.001$, $r = 0.991$). No correlation was found between egg size and abdomen size.

The highest rate of aggressive behaviour occurred in the only nymph and only female treatments, these two treatments being significantly different from the others (Figure 4A). Grabbing behaviour (Figure 4B) occurred more frequently when males were more abundant (range: 0-27 events in five minutes), as in treatments 0F/4M and 1F/3M, which were different from the other treatments. The highest frequency of coupling behaviour occurred in the treatment with equal proportion of sexes (2F/2M) but it was not significantly different from 1F/3M and 3F/1M. In the nymphal stage, coupling was not observed (Figure 4C). The interference behaviour (Figure 4D) was mainly found in the male biased treatment with a single female (1F/3M; range: 0-21 events in five minutes), which was significantly different to all other treatments.

DISCUSSION

The body size comparison between sexes shows that females are larger than males. Several non-mutually excluding interpretations may be put forward to explain this fact. The larger size of females may be associated with fecundity selection (Darwin, 1874; Presiozi & Fairbairn, 1996; Reeve & Fairbairn, 1999), since a bigger female can carry more eggs (Hedrick & Temeles 1989; Presiozi & Fairbairn, 1996). Interestingly, in our case female abdomen size correlated positively with fecundity (Figure 3).

Since carrying a male on her back during

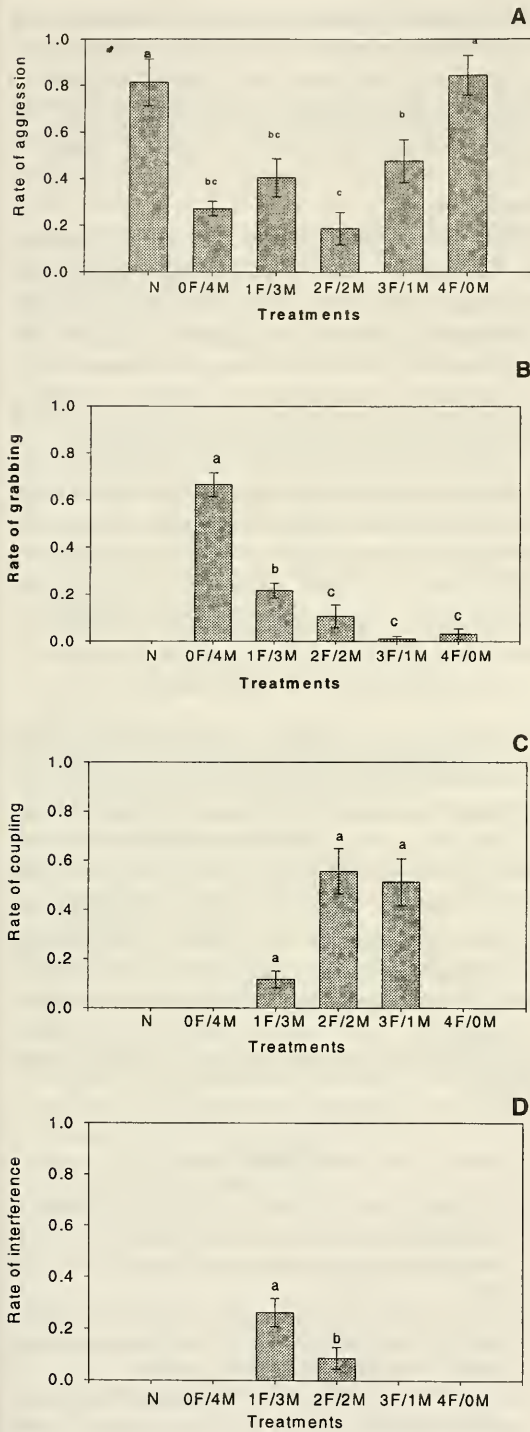


Figure 4. Comparisons of the different behaviours among the treatments. Ordinates represent the number of behavioural events of each given type divided by the total number of behavioural events displayed in each treatment. Abscises represent treatments with different sex ratios (F = Females, M = Males), or nymphs-only (N) treatment. See material and methods for the description of behavioural patterns.

coupling may imply a cost to the female, such as shorter life of paired female found by Fairbairn (1993) in the water strider *Aquarius remigis*, bigger females are less affected by such kind of costs. The smaller size of males may also be related to the copulatory behaviour (Rowe, 1994; Arnqvist *et al.*, 1996). The smaller size of males may also be related with copulatory capacity and sperm competition (Price, 1997; Parker, 1978; Rubenstein, 1989; Jablonski & Vepsäläinen 1995). Within the same genus, other studies have described that smaller males show more prolonged mating (Rowe & Arnqvist, 1996), and long mating is associated with a more effective fecundity and sperm displacement (Siva-Jothy, 1987; Arnqvist & Danielsson, 1999). Alternatively, the lower size of male may be associated with a higher mobility needed for female searching (Parker, 1978; Blanckenhorn & Fairbairn, 1995). Indeed, in the sex ratio treatments with a male biased proportion the frequency of behaviours related to search (i.e. grabbing and interference), was higher than in the other treatments (Figures 4B and 4D). Hence, the fecundity efficiency of a male appears to be negatively associated with its body size. Regardless of body size, males have bigger thorax, that can be due to allometric growth pattern or can be related with the presence of stronger muscles, which increase mobility and holding to the female during copulation. To our knowledge, no experimental evidence supporting this last hypothesis is available for water striders.

Another explanation to account for differences in body size is competition for resources (Darwin, 1859; Fairbairn & Preziosi, 1996). Larger organisms may be associated with aggression and dominance leading to efficient food acquisition. In our case, to the high proportion of aggressions found in the only-female (4F: 0M) treatment (see Figure 4A) can be associated to food territorial competition behaviour that suggest a possible positive selection in body size for females, but are necessary specific experiments to test this hypothesis.

Mating behaviour observed in the water striders may be dependent of sex ratio. By changing the sex ratio, as we did herein, it is possible to separate the intrinsic contribution of male and female behavioural patterns to the mating related behaviour (Vepsäläinen & Savolainen, 1995). Thus, mate searching behaviours can be reflected in grabbing (when the interaction occurs between individuals), and interference (which occurs between an indivi-

dual and an already formed couple and implies a more aggressive interaction). These two sexual behaviours were found more frequently in sex ratio treatments where males were predominant, and grabbing showed its maximum value in the treatment with only males. If grabbing is exclusive of one sex, it would be found more frequently in treatments biased to this sex. With this purpose, the experimental frequency of grabbing was compared with the expected probability to find grabbing at the different sex ratios treatments (calculated as the probability of encountering an individual of the same sex). A positive correlation between predicted probability and observed frequency of grabbing was found for males (Figure 5, $p < 0.005$, $r = 0.977$), while no correlation was found for females. Thus, grabbing behaviour is characteristic of males. Nymphs did not display grabbing or interference, probably because their ontogenetic stage is not focused in reproduction, so they direct most of their energy to food searching (Price 1997).

Usually, females allocate to reproduction a higher proportion of the energy budget than males (Greenwood & Adams 1987, Price 1997). Differentially, males invest in alternative strategies, such as strong competition between males for females (Speight *et al.* 1999). When the sex ratio is modified, mating opportunities are also modified (Vepsäläinen & Savolainen 1995), and differential investment to sexual behaviour can be shown. In the only male treatment the frequency of aggressive behaviours was lower than in the only female and only nymph treatments (Figure 4). Probably due to

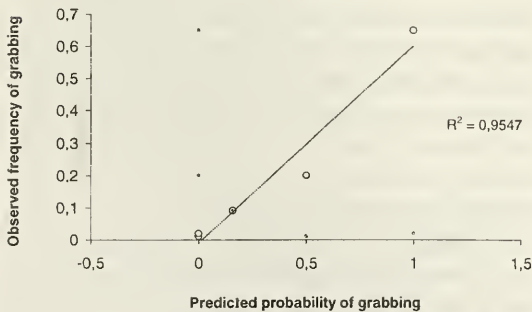


Figure 5. Relationship between the observed frequency and the predicted probability of grabbing. Ordinates represent the mean frequency of grabbing observed in each treatment. Abscises represent the predicted probability of grabbing for either sex in each treatment (males in filled circles and females in empty triangles).

the fact that the energy of males was focused on mate searching rather than food searching or territorial food competition behaviours and thus no sexual competition was established. Figure 4A shows a lower aggression frequency when the chances to mate were higher (more balanced treatments).

The behavioural results confirm that females invest more in reproduction in comparison with males, as seen in the weight differences and egg production. Hence, these results support the hypothesis that mate searching behaviour occurs mainly in the sex investing the smaller amount of energy in reproduction, the male in this case.

The functional relation of morphology and behaviour along the evolutionary process must be the focus of further research aimed at clarifying the differential importance of the ecological, phylogenetical and genetical basis of the maintenance of the patterns found in this work.

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