

## **Infection rates and pathogenicity of trypanosomatid gut parasites in the water strider *Gerris odontogaster* (Zett.) (Heteroptera: Gerridae)**

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**Summary.** Trypanosomatid flagellates are common protozoan gut parasites of a wide range of insect species. Water striders (Gerridae) harbour the trypanosomatid *Blastocrithidia gerridis*. Three different populations of the water strider *Gerris odontogaster* in northern Sweden were sampled to assess the infection rate dynamics of trypanosomatids. The initially very low infection rates (0%–15%) early in the season were followed by a rapid increase during the reproductive period of the water striders, reaching very high levels (80%–90%). The pathogenic effects of trypanosomatids on *G. odontogaster* adults were studied in laboratory experiments. The parasites caused a general reduction of host vigour. Male skating endurance was negatively correlated with the intensity of the trypanosomatid infection. However, infection of trypanosomatids increased the mortality among adults only when the water striders were subjected to food stress. The trypanosomatids did not reduce the fecundity of females provided with food. We suggest that trypanosomatid gut parasites may be an important mortality factor in water strider populations. Since the pathogenicity of the parasites is enhanced by stress, parasitism by trypanosomatids may contribute to the regulation of host populations.

**Key words:** Parasitism – Gerridae – Trypanosomatidae – Infection rate – Pathogenicity

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A wide range of arthropod species are known to harbour parasitic trypanosomatid protozoa in their digestive tracts (Wallace 1979). Although given considerable taxonomic, morphological and ultrastructural attention by parasitologists, trypanosomatids are largely ignored in ecological literature. Insect trypanosomatid gut parasites are generally considered to be nonpathogenic (e.g. Wallace 1979), despite the fact that some studies demonstrate that these parasites may indeed be pathogenic to

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their insect hosts (Bailey and Brooks 1972; Schaub 1988; Schaub and Breger 1988).

Water striders (Heteroptera: Gerridae) of many different species from all over the world are frequent hosts of trypanosomatid gut parasites (Patton 1908; Porter 1909; Becker 1923; Laird 1959; Wallace et al. 1960; Wallace et al. 1965; Wallace 1979; Tieszen et al. 1983; Tieszen and Molyneux 1989a; Tieszen and Molyneux 1989b). Laird (1959) provided a summary of the taxonomic literature, but some confusion still remains concerning the type species *Blastocrithidia gerridis* (Patton) and its developmental stages (Tieszen et al. 1983). Mixed infections of *B. gerridis* and other species of trypanosomatids (notably *Crithidia flexonema* (Wallace) and *Leptomonas collosoma* (Wallace)) seem to be common in many species of water striders, and cast some doubt on earlier taxonomic literature (Wallace et al. 1960; Wallace et al. 1965).

The trypanosomatids infect their hosts by ingestion, and pass through the fore- and midgut of water striders without attaching to the epithelium. Attachment occurs in the hindgut, and is followed by reproduction through binary division (Tieszen and Molyneux 1989a, b). The infection rates in natural populations may be very high, and the intensity of trypanosomatid infections can range from extremely heavy, where the intestine is gorged with parasites, and very light, where only a few parasites are present (Becker 1923; Tieszen and Molyneux 1989a, b).

In water striders, Patton (1908) suggested that transmission of trypanosomatid parasites occurs by cannibalism, and Porter (1909) suggested coprophagy. However, neither author carried out any experimental investigation of transmission. Tieszen and Molyneux (1989b) demonstrated in the laboratory that both *B. gerridis* and *C. flexonema* are transmitted via host water intake. Their results also indicated that the parasites could be transmitted by cannibalism. Transmission by cannibalism has been demonstrated in the congeneric species *B. triatomae*, a parasite of reduviid bugs (Schaub et al. 1989). Most likely, a combination of transmission modes oc-

curs in natural water strider populations (Tieszen and Molyneux 1989b).

This paper examines the infection rates of trypanosomatids in three different populations of the water strider *Gerris odontogaster* (Zett.), and provides the first study of the pathogenicity of the parasites. The effects of trypanosomatid infections on longevity, fecundity, and endurance of adult water striders were studied in the laboratory.

## Materials and methods

### Infection rates

*G. odontogaster* individuals were collected from three different localities near Umeå, northern Sweden (Holmsjön 63°46' N, 20°24' E, Gimonäsdammen 63°48' N, 20°19' E, and Trehörningsmyran 63°47' N, 20°22' E). The *G. odontogaster* populations at all three localities are monomorphic, macropterous, and univoltine. In order to estimate the temporal pattern of infection rates, samples were taken several times (see Fig. 1 for sampling dates) during May and June 1989. The water striders were anaesthetized with ethyl acetate in the laboratory, and carefully dissected under a stereoscopic microscope. The dorsum of the abdomen was removed, and the alimentary tract exposed. Infections occur primarily in the mid- and hindgut (Tieszen et al. 1983; Tieszen and Molyneux 1989a), and these parts were examined in vaseline-sealed coverslips. The alimentary parts were teased in 0.8% NaCl solution prior to examination. The intensity of the infection in each individual (the parasite load) was ranked according to a five degree scale: (0) uninfected individuals, (1) light infections, (2) moderate infections, (3) heavy infections and (4) very heavy infections (gut more or less occluded by parasites). The same methods of dissection and parasite load ranking were applied in the experiments described below.

### Parasite load and longevity

This experiment investigated the effects of parasite infections on male longevity. Males were collected from Trehörningsmyran on 30 May 1989. The water striders were introduced individually into 10-cm diameter glass jars in the laboratory, with a piece of floating cork (1.5 × 1.5 × 0.3 cm) serving as resting site. The males were divided into two groups with different food treatments. One group ( $n=65$ ) was fed daily with one frozen *Drosophila* fruitfly per individual for 15 days, whereafter they were fed once every 2 days. The second group ( $n=65$ ) was not provided with any food (starved). The glass jars were inspected every day and dead individuals were immediately dissected and the parasite infections were ranked. To examine whether size affects longevity, the length of the pronotum was measured in all individuals. When 50% of the males in each group were dead, the experiments were terminated and the remaining individuals were dissected and measured.

### Parasite load and fecundity

In order to assess whether trypanosomatid infections lower female fecundity, males and females collected from Trehörningsmyran on 30 May 1989 were introduced in pairs into plastic containers (30 cm diameter) in the laboratory. A piece of cork was placed in each container to serve as oviposition substrate and resting site. The oviposition substrates were replaced every third day, and the number of eggs was recorded. Each water strider pair ( $n=39$ ) was fed daily with four frozen fruitflies. The illuminated period was adjusted every day to correspond with the natural daylength. After 18 days all water striders (both males and females) were dissected

and the parasite infections were ranked. The length of each female pronotum was measured with a micrometer eyepiece, and the females were examined with respect to flight muscle histolysis since this is known to affect female fecundity (Kaitala 1989).

### Male endurance and parasite load

This experiment examined male endurance in skating against a water current in relation to the trypanosomatid infection level. Males were collected from Trehörningsmyran on 12 June 1989, and provided with food (frozen fruitflies) ad libitum prior to the experiment. The experiment was performed on 14 to 16 June.

A stream aquarium with a circular channel (diameter 54.0 cm and width 12.5 cm) was used. To prevent the water striders from climbing up the walls to rest, the walls were covered with an aluminium sheet. A pump generated a current in the channel (3.0 cm sec<sup>-1</sup>). Males ( $n=47$ ) were introduced individually into the stream channel. When introduced, they oriented towards the current and skated against it. However, the water striders could not fully compensate for the current, and so drifted with the current as a net result. To estimate the endurance in skating, each individual was observed for 5 min and the number of laps that it drifted with the current was recorded. After the experiment, the water striders were dissected and ranked for parasite load and the length of the pronotum was measured.

## Results

The trypanosomatids found in the alimentary tracts of *G. odontogaster* individuals examined were *B. gerridis* and *C. flexonema* (see descriptions in Wallace et al. 1960; Wallace et al. 1965). *B. gerridis* was most abundant. Mixed infections of the two species occurred in approximately 10% of the infected individuals, with *B. gerridis* as the dominant species in almost all cases.

### Infection rates in natural populations

The temporal pattern of infection rates was similar in all localities, i.e. a dramatic increase in the proportion of infected water striders among the overwintered adults from the beginning of May to the beginning of June (Fig. 1) (Chi-square test; Holmsjön:  $\chi^2=39.0$ ,  $df=1$ ,  $P<0.001$ , Gimonäsdammen:  $\chi^2=247.2$ ,  $df=3$ ,  $P<0.001$ , Trehörningsmyran:  $\chi^2=20.6$ ,  $df=3$ ,  $P<0.001$ ).

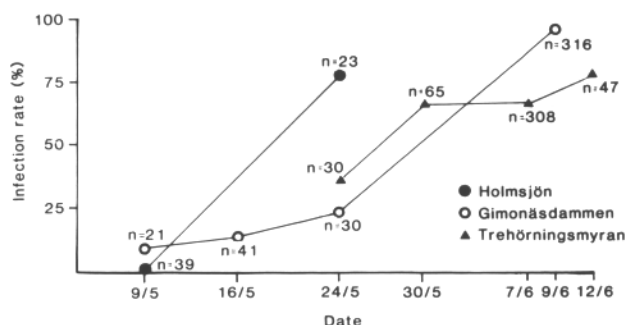


Fig. 1. The proportion of adult *Gerris odontogaster* individuals infected with trypanosomatids in three different populations in northern Sweden. The total number of individuals examined in each sampling occasion is indicated ( $n$ )

There were no significant differences between males and females in infection rates (Holmsjön:  $\chi^2=2.54$ ,  $df=1$ ,  $P>0.1$ , Gimonäsdammen:  $\chi^2=1.81$ ,  $df=1$ ,  $P>0.1$ , Trehörningsmyran:  $\chi^2=3.72$ ,  $df=1$ ,  $P>0.05$ ) or in frequency distributions of parasite load (Holmsjön:  $\chi^2=3.15$ ,  $df=4$ ,  $P>0.5$ , Gimonäsdammen:  $\chi^2=4.46$ ,  $df=4$ ,  $P>0.2$ , Trehörningsmyran:  $\chi^2=7.78$ ,  $df=4$ ,  $P>0.1$ ) in any of the three populations.

#### Parasite load and longevity

In the group of males that were starved, 50% of the males were dead after 5 days, whereas the corresponding period for the males that were fed was 24 days. In the group of males that were fed, the males that died during the experiment and the males that survived the experiment did not differ significantly with respect to parasite load (Mann-Whitney test,  $P>0.5$ ). However, in the group of males that were starved, males that died during the experiment had a significantly higher parasite load than those that survived (Fig. 2, Mann-Whitney test,  $P<0.01$ ). Further, among the starved males that died during the experiment there was a highly significant negative correlation between longevity and parasite load rank (Fig. 3,  $r_s=-0.495$ ,  $n=45$ ,  $P<0.001$ ).

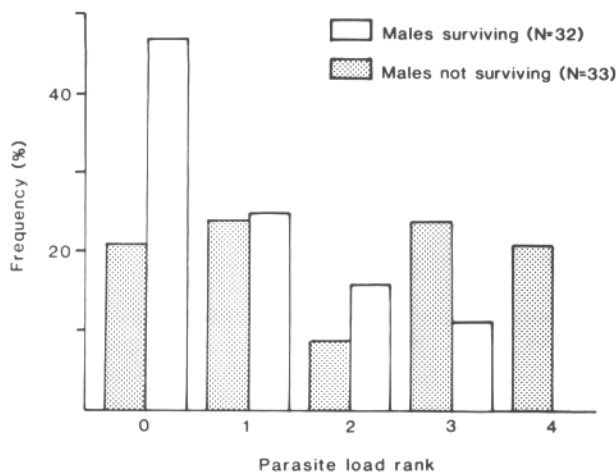


Fig. 2. Frequency distribution of the intensity of parasite infections (parasite load) of starved *Gerris odontogaster* males in the longevity experiment

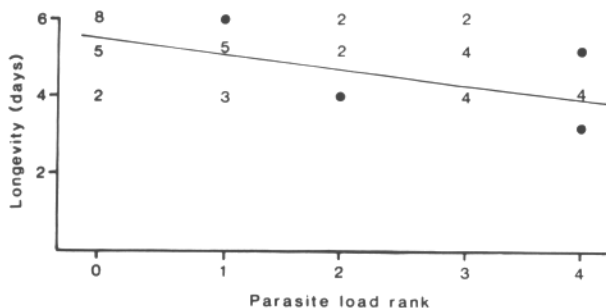


Fig. 3. The relation between parasite load and longevity for starved *Gerris odontogaster* males with known longevity ( $r_s=-0.495$ ,  $P<0.001$ ). Numbers represent the number of observations at each point

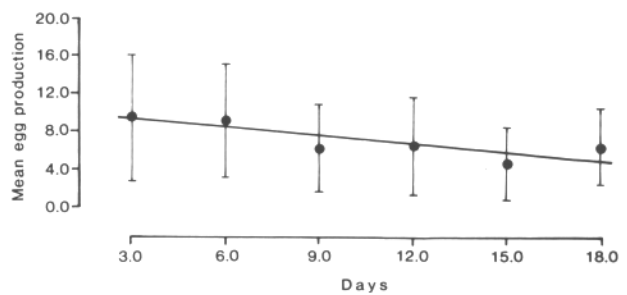


Fig. 4. Mean egg production ( $\pm$ SD) per *Gerris odontogaster* female per 3 days during the fecundity experiment ( $r_p=-0.249$ ,  $n=232$ ,  $P<0.001$ )

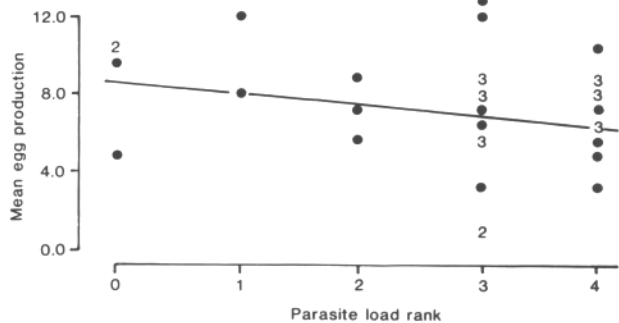


Fig. 5. Mean egg production per *Gerris odontogaster* female per 3 days in relation to the parasite load ( $r_s=-0.200$ ,  $P>0.1$ ). Numbers represent the number of observations at each point

There was no difference in size between males that died or survived during the experiment in either of the two groups ( $t$ -test,  $t=-0.02$ ,  $df=52$ ,  $P>0.5$  for fed males and  $t=0.74$ ,  $df=61$ ,  $P>0.4$  for starved males).

#### Parasite load and fecundity

The overall egg production rate of females decreased during the experiment (Fig. 4,  $r_p=-0.249$ ,  $n=232$ ,  $P<0.001$ ). The mean egg production per 3 days was not significantly correlated either with the parasite load (Fig. 5,  $r_s=-0.200$ ,  $n=39$ ,  $P>0.1$ ) or the size of the females ( $r_p=0.030$ ,  $n=39$ ,  $P>0.1$ ).

Further, within pairs, the parasite load of the females did not covary with the parasite load of the males ( $r_s=0.203$ ,  $n=39$ ,  $P>0.1$ ). The histolysis of flight muscles did not have any detectable effect on female egg production rate. Females with histolysed muscles (62%) did not differ from females with fully developed flight muscles in total egg production during the experiment (Mann-Whitney test,  $P>0.3$ ).

#### Male endurance and parasite load

Male endurance in skating was significantly affected by the parasite load (Fig. 6, ANOVA,  $F=3.25$ ,  $P<0.05$ ). Males with intense trypanosomatid infections were less able to oppose the water current. The size of the males,

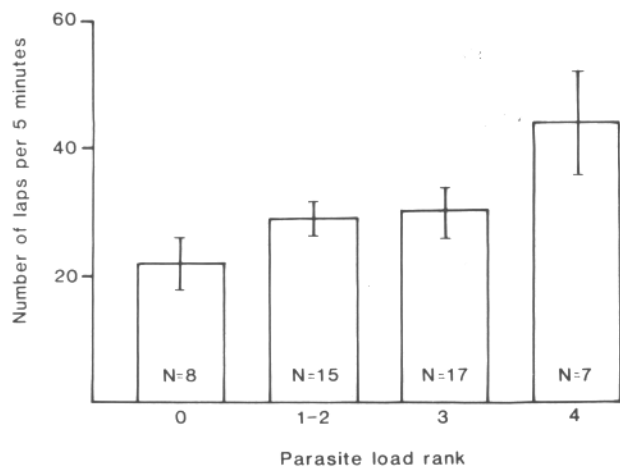


Fig. 6. The mean number ( $\pm$ SE) of laps that *Gerris odontogaster* males of different parasite load rank groups drifted downstream in a circular stream channel during 5 minutes (ANOVA,  $P < 0.05$ )

however, was not correlated with the number of laps they drifted with the current ( $r_p = -0.015$ ,  $n = 47$ ,  $P > 0.1$ ).

## Discussion

The transmission efficiency of the trypanosomatid parasites was obviously very high during late May and early June. A similar pattern, with infection rates (prevalence) in water strider populations rising rapidly to very high levels during late spring and early summer, was found by Tieszen and Molyneux (1989b). This presumably general pattern in water strider populations is most probably related to behavioural factors. During the reproductive period, interactions between water strider individuals, often of considerable duration, are very common. Activities such as mating, aggression, prey sharing, and cannibalism promote transmission of the parasites (Tieszen and Molyneux 1989b) and cause a rapid increase of the infection rates. This interpretation of the infection rate dynamics is supported by observations of moderate infection rates in the prediapause generation in late summer (Tieszen and Molyneux 1989b), in which the individuals interact much less.

Previous observations suggest that trypanosomatid infections may be retained in water striders during winter diapause (Tieszen and Molyneux 1989b). In agreement with this suggestion, the parasite load of infected water striders collected early in the season in this study was frequently very high, indicating that these individuals had been infected prior to winter diapause.

Contrary to the general assumption (Wallace 1979), our study demonstrates that trypanosomatid parasites are pathogenic to *G. odontogaster* adults. The parasites caused a general reduction of host vigour. The reduction in male skating endurance caused by the parasites may adversely affect e.g. the ability to acquire food and mates. However, the pathogenicity to water strider adults, especially in terms of reducing longevity, is obviously related to the degree of food stress. Fed water striders did not suffer notably from the infections in

terms of mortality, while parasite infections reduced longevity when the hosts were starved. Trypanosomatid infections did not affect the fecundity of water strider females provided with a constant food supply, although, by analogy with the effects on the longevity of starved males, the parasites may well reduce fecundity when females are under severe food stress.

Insect parasites often have their most severe detrimental effects on host fitness during the host's juvenile stages (Price 1980; Anderson and May 1981). Thus Schaub and coworkers have demonstrated that the trypanosomatid gut parasite *B. triatomae* is highly pathogenic to the larvae of several species of reduviid bugs (e.g. Schaub 1988; Schaub and Breger 1988). As with *B. gerridis* in water striders, the pathogenicity of *B. triatomae* is related to food stress (Schaub and Löscher 1989). Considering the effects of trypanosomatid flagellates on water strider adults, it is reasonable to assume that the effects on water strider larvae would be even more pronounced. It is known from previous studies of water strider populations that the mortality during the larval stages is very high (e.g. Spence 1986a; Zimmermann et al. 1982; Arnqvist 1989), and that trypanosomatids do infect water strider larvae (Tieszen and Molyneux 1989b). Thus, the effects of the parasites on larval growth and survival should be given attention in future studies. Trypanosomatid infections may also decrease survival during winter diapause, by reducing the nutritional status of water striders entering diapause.

Trypanosomatid flagellates may reduce host viability and the efficiency of the host's nutrient uptake in several ways. The parasites compete with the host for nutrients in the alimentary tract, and a massive infection of flagellates attached to the lumen of the gut is also a mechanical barrier reducing the receptive surface of the gastric lumen (Schaub and Löscher 1989). In addition, the parasites may disturb the host's excretion (Schaub and Schnitker 1988), and flagellates attached to the gut cause loss of microvilli in the gastric caecum (Tieszen et al. 1983).

Parasites which become more pathogenic when the host population is under stress are potentially important in host population regulation (Anderson and May 1981). Theoretical models have demonstrated that parasites with 'stress-induced' pathogenicity are capable of regulating their host populations, if the degree of stress is in any way related to host population density (Anderson 1979; Anderson and May 1981). This would be the case e.g. if food shortage becomes more pronounced at high population densities. We suggest that infections of trypanosomatid gut parasites may be an important mortality factor in many water strider populations, especially during the larval period. Further, since the pathogenicity of the parasites is enhanced by food stress, mortality caused by trypanosomatids should act in a density-dependent fashion and thus have considerable effect on water strider population dynamics.

With our growing knowledge of the organisms that interact with water striders, a far more complicated picture emerges of water strider population biology than was envisioned some years ago (e.g. Brinkhurst 1966).

Biotic interactions may profoundly affect water striders; aquatic predators (Spence 1986a; Arnqvist 1989; Zimmermann and Spence 1989), egg parasitoids (Spence 1986b; Nummelin et al. 1988; Arnqvist and Byström 1990), ectoparasites (Smith 1989), and endoparasites (this study) all have important effects. All these interactions may further affect water strider species asymmetrically, and they may thus have important impacts on local community composition (Spence 1986b, 1989; Smith 1989).

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