

Female territoriality in the waterstriders *Gerris najas* and *G. cinereus*

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Territorial behaviour of Fennoscandian *G. najas* was studied in nature and in the laboratory. Many of the reproductive females were territorial, while males and diapause individuals were not. In the field, the proportion of territorial females ranged from 1 to 24%. Territorial behaviour was common in the laboratory, where territories lasted on average for about an hour, and often for several or more hours. Moroccan *G. cinereus*, studied only in the reproductive season in the field, was similar in territorial behaviour to that of *G. najas*.

Territorial females of both species kept their positions in the current by striding upstream, and behaved aggressively toward alien individuals coming closer than 10-30 cm. Non-territorial individuals behaved aggressively only infrequently, and usually retreated if attacked. Territorial conflicts were usually won by the resident, but replacement of residents sometimes took place during the first half hour after the founding of a territory. Territories were frequently abandoned without fights. Individuals that abandoned territories often established new ones elsewhere either immediately or at some later time.

Males of both species ride upon the backs of females more or less permanently throughout the whole reproductive season and take part of the food caught by the female. Males stay attached to the female even when she dives down to the bottom of the river to oviposit under stones.

The function of female territoriality is probably defence of food supply. The patchy nature of the stream environment is likely to favour the evolution of food territories: insect food drifts downstream along definite lanes, and elsewhere food is more sparsely distributed. We also suggest that male riding behaviour is an ESS that secures repeated matings through the long reproductive season. Decoupling from a female would eliminate a male from the reproductive population.

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1. Introduction

Territoriality is common and widely distributed throughout the vertebrates, but it is regarded as much more patchily distributed among the arthropods (Wilson 1975, Itô 1981). Among these, territorial behaviour is best known from crustaceans and insects (Wilson 1975), and there is no doubt that territoriality in these groups will be found to be much more common than was previously suspected (Baker 1983).

Territorial behaviour may be classified, e.g., on the basis of forms of defence. However, to understand the evolution of territoriality a

functional approach may be preferable. Then the classification is based on the resource defended, thought to ultimately increase the fitness of territorial individuals. The two main types of resources defended by territorial insects comprise food and a mate. Food is a typical defended resource of insect females (but often also of males) and females receptive to mating, a resource of males (see Baker 1983). As for food intake, territoriality for mate acquisition is only an alternative tactic among a set of tactics. Which tactic or set of tactics is the best one depends on the pattern of the environment (Spence & Wilcox 1985).

The findings of Wilson et al. (1978) on female territories of a Costa Rican rivulet-living ripple bug (*Rhagovelia scabra* (Bacon), Veliidae), directed our attention to *Gerris*

¹The junior author takes full responsibility for the execution of the laboratory and field work.

(*Aquarius*) *najas* De Geer, the only North European Gerrid specialised for living in the ecologically similar, running-water habitat. Marked sexual dimorphism, spatially restricted movements of the females, and the fact that males ride upon the back of the same female for weeks on end (Huldén 1979) suggested female territoriality.

The strongest indication for possible female territoriality in *G. najas* is the structure of its habitat. In rivers and rivulets insect food drifting downstream on the water surface tends to be funnelled into a limited number of loci along narrow food lanes, while other parts of the river remain relatively devoid of food. Even though the exact location of good places may change in time, they typically remain fairly stable for days or even weeks (cf. Wilson et al. 1978). Such an environment, with food patchily distributed, should form an ideal background for the evolution of territoriality (e.g., Ricklefs 1979).

In this paper we present results of field and laboratory experiments on the territoriality of the Finnish *G. najas* and a closely related western Mediterranean species, *G. (Aquarius) cinereus* (Puton). Our objective was to describe the behaviour of the striders, although we made experiments designed to throw some light on the significance of female and male behaviour.

2. Material and methods

2.1. Field studies

The behaviour of *G. najas* individuals was studied in Keravanjoki, Hyvinkää (60° 35'N, 25° 01'E) and between Långträsk and Sumpen in Pohja (60° 07'N, 23° 27'E). Both are small rivers in southern Finland having dense *G. najas* populations. Similar observations on *G. cinereus* were made in the River Sousse in Aulouz, Southern Morocco (30° 30'N, 8° 10'W). All the rivers also harboured other species of waterstriders.

Observations in Hyvinkää were made on 7-8 May (sunny days after night frosts), and 20 May (overcast, +15°C), and in Pohja on 14 May 1983 (sunny weather), when overwintered imagoes had moved from the land to the river but no nymphs had yet been produced. The work in Morocco was done on 27-28 May 1983 (sunshine), when at least some of the offspring imagoes had moulted. It is clear that the different periods of field work make comparison of the sites difficult. Rather the results should give a general impression of the variability of behaviour.

Observations were made using binoculars, and the waterstriders thus remained undisturbed. The individual or pair to be followed was chosen without any specific criteria, and its behaviour then recorded during at least

five encounters with other individuals. Both attachment to the site and swimming at/chasing/lunging at/jumping on approaching conspecifics (here collectively called aggressive behaviour) were observed before the individual was regarded as being territorial. Overall, the behaviour of 678 pairs, 201 single males and three single females was recorded.

When no spontaneous encounters were recorded during prolonged observation, the pair being followed was tested for territoriality by throwing one alien individual at a time into its immediate vicinity. At least one of the alien individuals was a female.

We also counted the number of males and females in groups which stayed in the same restricted area, as well as the number of encounters taking place among individuals. Likewise, the proportion of feeding individuals was recorded.

2.2. Laboratory experiments

An experimental stream with a 5 m/min. current, rotating anti-clockwise, was constructed in a oval plastic basin. The width of the river was 0.5 m and length 3 or 8 m, depending on whether encounters among individuals or the permanency of territories was being studied. During the latter studies the striders were restricted to a U-shaped (8 m) space instead of a straight stretch (3 m) on one of the two longer sides of the oval basin.

The vertical sides and the bottom were made of plastic, and the bottom was covered with sand. Bricks (5 for the 3-metre long river, and 11 for the U-shaped one) were placed at the bottom perpendicularly to the current. One end of the brick projected a few centimetres above the water surface, and the other end was submerged as much below it. The temperature of the experimental river was +17°C, and the daily illumination rhythm L20:D4.

For other purposes several trout, about 10 cm long, were kept in the same basin. The possible effects of the trout upon the behaviour of the waterstriders were not known, but twice an unsuccessful attempt by a trout to catch a waterstrider was observed. No waterstriders disappeared during the experiments, however.

The experimental adults, 33 females and 37 males, were collected in the middle of June from the River Kligavälsån in Scania, South Sweden. All the individuals were overwintered ones and in the midst of the reproductive period of the population.

To study possible changes in behaviour, all individuals were marked individually with spots of paint on the thorax. Because of the prolonged attachment of males to females, individual recognition of the female was mainly based on the male on the latter's back. If it is agreed that the same male-female combination at the end as at the beginning of the observations indicates no change of partner during the experiment, our procedure should not bias the results. That this holds true is supported by long-term observations of marked couples in the field (Huldén 1979).

Our experiments were planned to study aspects of territoriality in *G. najas*: Firstly, the location and permanency of territories relative to food was tested. The waterstriders were kept without food for one day and then observed for the following 10 hours. During the next 10 hours, ten vestigial-winged fruit flies (i.e., on average 1 per 7 waterstriders) were added every 15 minutes to the upper end of the rivulet. The locations of all individuals were checked every 15 minutes.

The behaviour of individuals, which were more or less site-tenacious on the free water surface, was studied carefully. It was generally clear within one minute whether the individual or couple in tandem (cf. chapter on male behaviour) was really site-tenacious and defending its site. Female defence took the form of swimming toward approaching individuals and chasing them away. Males did not take part in defence.

Secondly, in order to bring to light possible differences in behaviour between territory owners and non-territorial couples, encounters among tandems were studied. Altogether 26 couples were monitored during one day. Vestigial fruit flies were added to the rivulet *ad libitum*. A minimum of 10 encounters per tandem was recorded.

After the completion of the experiments all the waterstriders were preserved in 70% ethanol. To study sexual dimorphism for size and possible size differences between territorial and non-territorial individuals, the length of the body and the mesothoracic femur was measured on the preserved individuals ($n=70$) with a binocular microscope to an accuracy of 0.2 mm. Measurements on *G. cinereus* were taken from field-collected individuals.

Because females could not always be recognised individually, as the male on their backs covered their markings, only females which could be directly identified on the basis of the marking, or which were attached at the end of the experiment to the same male as at the beginning, were considered for purposes of comparison.

3. Laboratory results

3.1. Male behaviour

Single males tried to climb upon the backs of any waterstrider encountered, irrespective of the latter's sex or whether it was coupled or not. The majority of *G. najas* imagoes were attached as couples (but not necessarily *in copula*). Such couples are henceforth referred to as tandems or simply females. When necessary, females not in tandem are called single females.

Males rode upon the backs of the females so that only the tips of their hind legs touched the water surface. Thus, the locomotion of tandems was totally provided by the females. Also, both individuals consumed prey caught by the female. Males were never territorial.

3.2. Oviposition

Many females were observed to dive below the water surface and crawl on the bottom to oviposit. Each time the female had a male on its back, but not once was a single female seen to dive. As 20 of the 26 females in tandem dived, but none of the 7 single ones, the

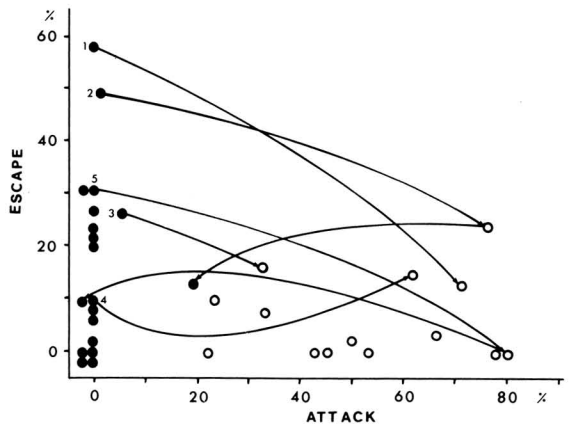


Fig. 1. Behaviour of *Gerris najas* tandems. The abscissa gives for each female the percentage of aggressive behaviour ("attack") and the ordinate of escapes due to aggression by another female. The two percentage values added to neutral encounters (not shown) add up to 100%. Several females (numbered) switched behaviour between territorial (circles) and non-territorial (dots) modes. The data come from laboratory experiments with food supplied *ad libitum*.

difference in diving behaviour for oviposition is statistically highly significant between the two groups of females ($P=0.0008$, Fisher's exact test).

3.3. Encounters among females

Most individuals in the experimental stream actively maintained their position by facing upstream and skating against the current. Of such tandems, 14 out of 26 behaved aggressively, i.e. they were territorial in the strict sense (e.g., Wilcox & Ruckdeschel 1982). Over 20% of their encounters with alien individuals were aggressive, and they seldom withdrew when faced by other females (Fig. 1). Defended areas extended approx. 30 cm upstream and approx. 15 cm laterally from the territory owner, facing upstream. This is a rough estimate of territory size, as no exact measurements were made.

Several hundred territorial conflicts were recorded. Aggression was observed when non-territorial imagoes skated into defended territories. Also aggression occurred between territory owners when transgressions took place. A female defending her territory skated toward an intruder, who then usually withdrew before physical contact took place.

Aggression was especially directed against waterstriders upstream from territory owners. However, a territorial tandem often allowed another tandem to drift or skate close by parallel to the current.

Territorial females in tandem were aggressive towards females and also towards single males. Single females seemed to behave similarly to those in tandem. However, because single females are rare in nature during the reproductive season, our studies were concentrated on tandems.

Aggression was rarely seen among non-territorial individuals, and most of those gave way to approaching gerrids. Their only aggressive encounters (females 2 and 3 in Fig. 1) are based on single observations, and the reason for the behaviour remained unknown. (Note that there are 3 and 2 points in the figure, for females 2 and 3, respectively, and those for the non-territorial phase are on the far left.)

Several females changed their behaviour during the observation period. Irrespective of whether the female changed from being non-territorial to territorial (5 tandems, no. 1, 2, 3, 4 and 5 in Fig. 1) or vice versa (no. 5 later on, and no. 2), their non-territorial behaviour could not be distinguished from the non-aggressive behaviour of those females which were non-territorial throughout the whole experimental period.

3.4. Permanency of territories

We observed the founding of a total of 37 territories within a period of 20 hours. The territory founder was always a female, and only three times was it single.

All the territories were located at the source part of the laboratory stream, and none were founded in the downstream ends of the 8-metre long, U-shaped river. All 11 territories, which lasted for over one hour, were found within the uppermost 3 metres. Instead of territories the down-stream part of the "U" was occupied by a flotilla consisting of 10 to 20 tandems. These were nonaggressive towards each other, and did not keep to any particular site in the river. They moved around quite freely, especially within the last 3 metres of the U-basin.

The maximum number of simultaneous territories was six, but usually ranged between three and four. When no food was in the river,

the median duration of a territory was 30 min ($n = 19$, range 10–225 min), and when food was supplied, 15 min ($n = 18$, range 5–435 min). The difference is not statistically significant (Mann-Whitney U -test). However, without food a territory lasted for a maximum of 3.75 hrs, but with food added the most persistent territories lasted for 7.25 and 5.50 hrs and were still existing when the experiment was ended. Both territories were located at the very mouth of the river.

3.5. Does the resident always win?

During studies on the permanency of territories, we recorded 22 abandonments of territories classified as occurring without any obvious reason. This was partly due to our observation method, which was based on checking the situation every quarter of an hour. In 22 cases the territory site was empty. We actually observed voluntary abandonment three times. Abandoning females simply drifted downstream, to join the flotilla of non-territorial individuals (one climbed upon a brick to rest). There they behaved nonaggressively like the individuals they had joined.

But an interesting question is: does the resident always win? In contrast to territorial males of the speckled wood butterfly *Pararge aegeria* (L.) (cf. Davies 1978), the answer for *G. najas* is definitely no. We recorded 4 take-overs of territory. It seems notable that all the observed territorial displacements took place during the first 10–30 minutes of the founding of the territory.

3.6. Size distributions

The size distributions of territorial and non-territorial females were very similar, and no statistical significance between the groups could be shown for the parameters studied. The same was true when single males and males attached to non-territorial females were compared with males upon the backs of territorial females.

The males were about one quarter (in *G. cinereus* about one third!) smaller than the females, and the difference between the sexes is statistically very significant. The female to male ratio is 1.3 (in *G. cinereus* 1.4–1.6) for body length, and 1.2 (1.3–1.4) for femur length.

4. Field results

Only occasional females were not in tandem. At the beginning of the season 1% of the females at Hyvinkää were territorial. Two weeks later, on 20 May when the majority of females had hypertrophied abdomens full of eggs, the proportion was 6%. At Pohja 24% of the females were territorial (females with hypertrophied abdomens), and in Morocco 8% behaved territorially (females full of eggs). Females maintained their position by striding toward the current. The proportion of tandems not attached to groups was similar to the proportion of territorial females of all females. Non-territorial females tended, in contrast to territorial ones, to occur in groups.

Practically all the females had a male on their back. As the ratio of males to females varied between 1.5 and 1.1, depending on the river and/or season, part of the males were single (the number of imagoes observed per locality and day was 215-480 in Finland and 181 (2 days) in Morocco). These were mainly occupied in search for a mate and tried to become attached to any waterstrider they happened to encounter, irrespective of its sex or species, or whether it was already in tandem or not. The males, on the other hand, did not attach to any specific site, nor did they indulge in chasing other individuals for any other evident reason than to climb upon their back. Accordingly, while the females, usually in tandem, were often territorial, the males were not.

The more or less permanent attachment of *G. najas* males to the backs of females for several weeks (see also Huldén 1979) is a unique feature known among the European Gerridae species (although we expect the same behaviour in *G. cinereus*). Just as unique is the habit of the female of diving to the bottom to lay her eggs on stones, and even then the male accompanies the female (see Sect. 3.2.). As diving for oviposition is vital for successful reproduction in a habitat with a highly fluctuating water level, it follows that territorial defence will be interrupted after a few days (see Huldén 1979). The impact of egg-laying dives on territory dynamics is, however, not known.

The percentage of feeding pairs varied between 0.5 and 10% (both extremes being observed at Hyvinkää), indicating temporal variation of food resources in the river. As the

function of territorial behaviour seems to be improved food intake, it is crucial to compare success in the capturing of prey by territorial and non-territorial females. While scanning through tandems with food during our field studies, we obtained the ratio of 2 feeding couples to 22 non-feeding ones in territorial striders, and 4 to 68 in non-territorial ones. The data are too limited for statistical inference.

5. Discussion

We can think of four potential proximate reasons for the territoriality of *G. najas* and *G. cinereus* females. These are (1) food, (2) mating, (3) parental defence of nymphs, and (4) protection of egg batches. We will discuss these in sequence and show that the role of food is likely to be a crucial one, and that there are sound reasons for rejecting the remaining ones.

(1) When food was added during the experiment, the territories lasted longer than when the striders were kept without food. Even though the difference was not statistically significant, the result lies in the direction expected on the basis of the pattern of the environment: the drifting food is funnelled through limited passages in the stream, while other sites remain relatively void of food. This supports the hypothesis that food is the proximate determinant of female territoriality in *G. najas*. The same mechanism was described from a tropical ripple bug species, living in a similar running-water environment (Wilson et al. 1979). Likewise, individuals of *G. remigis* Say — the North American ecological equivalent of *G. najas* — are territorial for food. But in contrast to the European species, both sexes are territorial (Wilcox & Ruckdeschel 1982).

(2) The permanence of male-female tandems and the lack of male territories (even though waterstrider males are the active sex in initiating mating, while females decide whether to accept a male or not), give reason for rejecting the hypothesis of mating territories in *G. najas* and *G. cinereus*. This does not mean that a female occupying a good territory could not obtain a high-quality male, but possible hierarchies among males in the acquisition of territorial females have not been studied. However, the bases for territoriality of

G. najas/cinereus and *Limnopus rufoscutellatus* (in which the male is territorial, Vepsäläinen & Nummelin 1985) are strikingly different. The function of territories in the latter species seems to be the acquisition of mates (Vepsäläinen 1985, Vepsäläinen & Nummelin 1985; see also Spence & Wilcox 1985 for similar results on two Nearctic *Limnopus* species).

(3) In nature, imagoes and the youngest nymphs are segregated by habitat: while the imagoes thrive in a moderate current, the nymphs concentrate in lentic lagunae usually downstream from the imagoes (our own unpublished observations). Hence, the hypothesis of territoriality existing in order to protect nymphs appears to be untenable.

(4) 19 out of 21 egg batches were deposited under bricks on the bottom of the experimental rivulet in the laboratory. It is thus unlikely that the female could in any way protect its egg batches against occasional predation.

Wilcox & Ruckdeschel (1982) were able to demonstrate both lower and upper food thresholds for the territoriality of *G. remigis* individuals. As our experiments were not designed to study thresholds, a comparison among the closely related stream-dwelling striders will have to remain open. However, although food seems to be the proximate reason for territoriality in both species, the way in which it affects fitness may be different. Territoriality in *G. najas* is restricted to reproductive (i.e., overwintered) females, which typically have a male attached to their backs more or less permanently throughout the reproductive season. In *G. remigis*, both reproductive and diapause males and females, and additionally the three final instar nymphs, are territorial (Wilcox & Ruckdeschel 1982). A closer comparison between the two species might prove rewarding.

It is tempting to believe that the size of females is correlated with their success in founding and/or conquering territories. However, our laboratory results indicate that the duration of occupation and/or recent success in territorial defence by the female plays an overriding role: once a female had been in her territory for over half an hour, its replacement by other females seemed practically impossible. During the first 10 to 30 minutes a territorial female may be displaced; evidently, the building-up of 'self-confidence'

takes some time. Thus, while our results emphasise the role of experience in keeping the territory, they are not in complete harmony with Davies's (1978) results on the speckled wood butterfly, in which the resident is said always to win. On the other hand, our results are in agreement with the model by Maynard Smith & Parker (1976). This makes the point that contests in nature are mostly asymmetric and settled quickly. The model also predicts that this is the case irrespective of the strength of the contestants. However, escalated contests (and displacement of territory owners) may occur when information about the asymmetry is imperfect, i.e., during the early period after establishment of territories.

The insignificance of size in settling territorial contests raises the question of how extreme sexual size dimorphism evolved in *G. cinereus* and *G. najas* to produce a much larger female than male. In the male-territorial *Limnopus* species the opposite evolution for an extremely slight size difference between female and male (or an even larger male) could be explained by selection for dominance coupled with larger size (Spence & Wilcox 1985). A dominant male need not always be territorial, and in fact there seem to be environmental states that favour other modes of behaviour to that of territoriality (Spence & Wilcox 1985; see also Hayashi 1985 for the Japanese *Gerris elongatus* (Uhler)).

Thus, size patterns of the two sexes can plausibly be explained in *Limnopus* species, where the male may have the advantage of size in several competitive (not only territorial) environments for acquiring a mate. But this explanation does not work for *G. najas/cinereus*, the female of which behaves non-aggressively soon after she has abandoned her territory. We therefore suggest that enhanced sexual size dimorphism is not a result of selection for larger size in females but of smaller size in males.

A single male *G. najas* does not court a female but tries to mount immediately it comes in contact with one. In this respect the male would be in similar situation to the so-called "sneaky rapists" (SR) males of Nearctic *Limnopus*, which, in contrast to other patrolling males and territorial ones do not signal. Spence & Wilcox (1985) emphasize that small males may be particularly suited for the SR tactic because they appear to be more difficult for females to dislodge through active

resistance. Without a doubt small male size, by decreasing energy costs of a female in tandem, is advantageous for both sexes, measured directly by the number of offspring. The costs of striding upstream while keeping a territory may be high enough to explain the female's alternation of territorial behaviour (for catching food) and spending periods in dense flotillas in lentic lagunae.

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