

## Male territoriality in the waterstrider *Limnopus rufoscutellatus*

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Territoriality in *Limnopus rufoscutellatus* (Gerridae) was studied both in the laboratory and in nature. Some reproductive males defend territories of approx. 50 cm in radius, while females and diapause males are not territorial. Territories usually lasted about a day in nature, but in the laboratory persistences of up to a week were recorded.

Territorial and non-territorial males send surface wave signals. Males are chased away from territories by the territory owners, but females are approached for mating. As a rule, a male resident on his territory wins a conflict with other males. The duration of territory occupation and/or success in recent male-male interactions, and not size, seems important in getting the upper hand in conflicts.

We suggest that the function of male territoriality in *L. rufoscutellatus* is to increase mating success but not food intake. As males alternate between territorial and non-territorial modes of behaviour, and also non-territorial males try to mate, territoriality is only one of the alternative male mating tactics.

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### 1. Introduction

During laboratory experiments designed to study surface wave communication among waterstriders (Nummelin 1982) and habitat segregation among their developmental stages (e.g. Vepsäläinen & Nummelin 1986), stationary males of *Limnopus rufoscutellatus* (Latreille) emitted surface wave signals as described for several other species of gerrids by Wilcox (1972, 1979).

The behaviour indicates male territoriality in *L. rufoscutellatus* (cf. Spence & Wilcox 1985, Wilcox & Spence 1985). The purpose of this paper is to describe the territoriality of *L. rufoscutellatus*, and to relate it to the surface wave communication of the species.

### 2. Material and methods

#### 2.1. Laboratory experiments

Individuals for study were collected from nature in two groups. The first one consisted of 36 males in the post-winter reproductive stage collected in the reproductive

season before midsummer, and the second group of 17 pre-winter diapause males collected in early September. All individuals were from the vicinity of the Tvärminne Zoological Station on the southern coast of Finland. Additionally, equal numbers of reproductive and pre-winter females were collected and used in the experiments with the males.

All males were marked individually with small coloured spots (see Matthey 1974), but females were left unmarked.

Round plastic basins with a diameter of 120 cm were used as experimental ponds. Six round, equally spaced wooden plates with a diameter of 10 cm were anchored on the water surface and served as resting places and potential territory centres for the waterstriders. In each experiment, 10 to 20 males (i.e., densities of about 8.8–17.7 ind./m<sup>2</sup>) and equal numbers of females were used. The hind wings of all individuals were cut to prevent them from flying. Food was kept superabundant.

The behaviour of the striders was observed from a distance of 2 metres through binoculars to minimize disturbance. A special effort was put into describing encounters among males. The observed number of male-male encounters was  $16 \pm 11$  ( $\bar{x} \pm SD$ , minimum 5) for reproductive males, and about 10 for diapause males. Each male was followed individually for up to half an hour to obtain the chosen minimum number of five encounters. The number of encounters recorded among males totals 778.

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

As territoriality is defined as defence of a fixed area against conspecifics (intraspecific territoriality) or other species (interspecific territoriality) (Itô 1981), we recorded for each male: (1) whether he was site-attached or not, (2) whether he behaved aggressively toward the other male or whether he escaped when attacked, and (3) the possible sending of a high-frequency (HF) surface wave signal before or after attacking (or being attacked) (see Nummelin 1982). In this study HF signalling was distinguished from other signalling and activities by naked eye as being a rapid series (frequency ca. 25 Hz, duration ca. 0.5–3 sec) of powerful thrusts of body perpendicular to the water surface. Courtship (CS) signalling by a male when encountering a female is visible as a much slower-paced waving of the body (ca. 3 Hz, >1–5 sec). Low-frequency (LF) waves (ca. 10 Hz, <1 sec) originate when an individual attains 'threat' position, raising high on its legs and tapping the water surface for a while with moderate pace.

Aggressive behaviour was defined to include an attack on another individual (either swimming at/chasing/lunging at/jumping on approaching striders). Escape was defined as withdrawal when attacked. When no attack or withdrawal was observed but one or both males seemed just to move on, the behaviour was defined as neutral.

The persistence of territories was studied by daily checking the position and status of the males in the basin.

To study the relation between male size and success in territorial encounters, the lengths of the body, and the mesothoracic and hind femurs of 35 males were measured with a binocular microscope ( $\pm 0.2$  mm). Their live masses were measured with a Mettler balance ( $\pm 0.01$  mg). The status of all measured individuals was known: 15 were territory owners, while 20 were not.

As it is conceivable that sex-limited territorial behaviour may affect sexual dimorphism for size, the lengths of the body, and of the mesothoracic femur and the proboscis were also measured on 10 males and 10 females.

To study the locomotory activity of the striders the experimental basins were divided into 12 squares of about 950 cm<sup>2</sup>. The square contours were marked on the bottom, and the total number of transgressions from one square to another by the individual being followed was recorded per time unit.

The effect of food on the founding of a territory was studied by a simple one-day experiment. Food was abundant but locally delimited to one quarter of the test basin (called the restaurant) with 2 territorial and 9 additional non-territorial males. The territories were located outside the restaurant. The foraging behaviour of the males and possible founding of new territories were recorded.

## 2.2. Field observations

Densities of early summer males and females were studied daily in different-sized ponds by individual marking, release and recapture in southern Finland in the period 3–12 June. The locations of the individuals were marked on a map. The area of the largest pond was ca. 370 m<sup>2</sup>, and those of the smaller ponds ca. 100 and ca. 70 m<sup>2</sup>.

The turnover of males and females in the ponds was calculated from the equation  $T = 100(E+I)/(S_1+S_2)$ , where  $S_1$  and  $S_2$  are the total numbers of individuals observed on the two successive days, and  $E$  and  $I$  are the numbers of individuals unique to the first and the second day, respectively. If an individual was observed on the  $i$ th

and ( $i+2$ )nd day in the same pond but not on the day between, it was nevertheless judged to have been present that day. Daily turnover was estimated in the large pond in the period 3–10 June and in the smaller ones on 5–10 June.

The behaviour of individually marked males was followed in early summer in five ponds near the Tvärminne Zoological Station. The size of the ponds ranged from 3 to 50 m<sup>2</sup>.

During 24 days, in the period 22 May–17 July, the behaviour of male striders was followed at least two hours per day in a 15 m<sup>2</sup> pond. One male was observed at a time to obtain results on ca. 10 male encounters per selected individual.

## 3. Results of laboratory experiments

### 3.1. Females and diapause males

Female aggression was rare, and females were not site-attached. As a rule they avoided approaching males by skating off. Only three times was a female seen to chase away a male attempting to mate.

None of the 17 diapause males studied behaved aggressively towards other males. The only attack on a female was observed when a male tried to catch the prey she was devouring.

### 3.2. Reproductive males

The following three types of behaviour occurred when reproductive males met: (1) attack, (2) escape, and/or (3) emittance of an HF-signal. Aggressive behaviour was mostly connected with the defence of a territory measuring about 0.5 m in diameter.

Territorial males behaved aggressively in at least 10% of their encounters with other males. On a territory, they were attached to a fixed place (usually by one mesothoracic leg to one of the wooden plates). After an attack, males returned to their territory centres. Only two males did not return, but switched to a non-aggressive mode of behaviour, skating around in the basin. Usually encounters were decided on the basis of a single attack by the territorial male, who invariably won the contest.

The result was more complicated in territorial fights involving repeated attacks and escapes lasting up to 2 minutes. Such interactions were noted twice in the laboratory and once in nature between males of territories bordering each other. Generally, aggressive

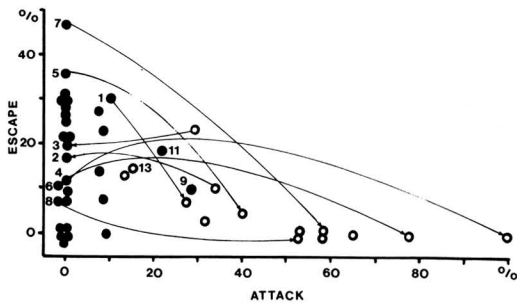


Fig. 1. Proportions of attacks and escapes of individually marked males in laboratory experiments with abundant food (the two modes of behaviour together with neutral behaviour, not shown in the picture, add up to 100 percent). Individuals which switched behaviour between territorial (circles) and non-territorial (dots) modes (exceptions: no. 9, 11 and 13) are numbered.

males did not escape, and non-territorial males did not attack. Fig. 1 summarises the attack and escape frequencies of each territorial and non-territorial male, and shows that there were exceptions to the rule.

The exceptions consisted mostly of single, unexplained attacks by non-territorial males or single escapes by territorial ones. However, male no. 13 ( $\sigma$  13), which had a broken hind leg, escaped several times without losing its territory. This indicates that a territory is not always accepted by the intruder even though the territory owner is driven away for a while. The non-territorial  $\sigma$  11 behaved exceptionally by attacking repeatedly without any obvious reason, but the frequent attacks by  $\sigma$  9 took place during a fight over a territory with  $\sigma$  3 that won the contest.

Repeated attacks and escapes by the non-territorial  $\sigma$  1 were also observed. This male later changed from a non-territorial to a territorial mode of behaviour. Seven other changes were noted during the study period: two males ( $\sigma$  2, 3) gave up their territories and behaved thereafter nonaggressively, and five males ( $\sigma$  4–8) founded territory later, and only then behaved aggressively (Fig. 1).

### 3.3. Signalling

When two males met each other, they emitted an HF-signal in about 22% of all observed encounters. Clearly, signalling was not restricted to territorial behaviour, as non-

territorial males ( $n=28$  encounters) sent the HF-signal equally as often as the territorial males ( $n=16$ ) did.

Individual differences in signalling were, however, large, and the timing of signalling appeared to differ between territorial and non-territorial males: signalling usually preceded attack but followed escape.

### 3.4. Effect of recent success

Our data allow us to generalise that a territorial male always wins contests against alien individuals. Size comparisons between territorial and non-territorial males (below) do not indicate clear-cut size-correlated advantages in founding a territory. It is plausible that a male's success improves with ownership of a territory and/or his success in male-male interactions on his territory. The following short experiment implies that this may be true.

15 males were introduced into the experimental basin and observed for 5 hrs. After the first male had founded a territory and defended it successfully (for this, at least 5 successful and no unsuccessful fights were required), it was removed from the basin. When a second male turned territorial, it was again allowed to defend its territory successfully. Then the first male (which had temporarily been removed) was reintroduced to the basin. It was, however, unable to displace the present territory owner. After the second territorial male was removed, a third one founded a territory, and defended it successfully in spite of reintroduction of the former territorial male.

### 3.5. Sizes of territorial vs. non-territorial males

We also measured the whole body lengths of the above 15 males. Of the three territorial ones, the first male in the territory succession was the smallest one, while the second male was the largest. The 12 non-territorial males included the basin's largest male and two males of similar size to the biggest territorial male.

Another series of measurements of 15 territorial males (taken for measuring when territorial) and 20 non-territorial males (never observed to be territorial) did not reveal statistically significant differences between the two male groups for lengths of front, middle and hind femurs, breadth of thorax, total body length or live mass.

3.6. Persistence of territories

We have data on the duration of 15 territories. The maximum persistence of a territory in an experimental basin among the same males and females was one week (5 records), and median duration 3 days. Due to the experimental design it was not possible to observe longer persistences, as the basin was washed and the striders changed once a week. Likewise 2 territories which lasted for 3 days and one for 4 days were destroyed due to the experimental design. Shorter, absolute durations of territories (abandoned before termination of the experimental run) were recorded as follows: 5 days (1 case), 3 d (1), 2 d (3) and 1 d (2).

A return of males to their territories after a sudden but short disturbance was tested by shaking the basin vigorously so that all the waterstriders left their sites. The intervals between 3 subsequent disturbances were about half an hour. The 5 territory owners (two and three individuals per basin) returned to their sites within some minutes of each disturbance.

3.7. Locomotory activity

Territorial males moved less than non-territorial ones (territorial:  $0.27 \pm 0.11$  transitions/min; non-territorial:  $0.96 \pm 0.64$ /min, respectively; Student's  $t = 3.36$ ,  $P < 0.01$ ,  $df = 18$ ). Of course, the activity of territorial males depends on population density. In our experiments the density was high, causing frequent checks on approaching individuals by territorial males.

3.8. Frequency of male encounters with females

We compared the frequency of female encounters by territorial and non-territorial males by observing one male at a time for 5–35 minutes. In a total density of 8 striders/m<sup>2</sup> and with a female to male ratio of 2, non-territorial males encountered females on average about twice as often as did the territorial males (the difference between the two behavioural groups is statistically highly significant). In densities of 0.2–0.3 females to one male (total density 3–6/m<sup>2</sup>), non-territorial and territorial males encountered females with about equal fre-

quency. For both behavioural groups the decrease in encounter frequencies is statistically highly significant. But when the decrease is for non-territorial males approximately proportional to the drop in female numbers per male, the decrease is slower for territorial males (the difference in the change of encounter rates for the two male groups is statistically highly significant).

We also recorded the attempts of males to mate with females. Most often the female escaped before the male came close enough, and hence our data is scanty. No difference in trial rate was revealed between territorial and non-territorial males at either density, and all trials were unsuccessful.

3.9. Effect of food

The first territory owner to enter the delimited food area (the restaurant) brought the food item back to his territory. The other territorial male consumed his food in the restaurant, and returned to his territory after half an hour, chasing away other males within the territory. The restaurant through the whole experimental day was in constant use, several males often visiting it simultaneously. However, none of the 11 males in the basin founded a territory in the restaurant quarter, neither did the non-territorial ones establish one elsewhere.

3.10. Sexual dimorphism

Females are bigger than males (Table 1), as in most waterstrider species. Using mean body, mesothoracic femur, and proboscis lengths, the estimated female to male ratios ranged between 1.03 and 1.09. The coefficients of variation of male femur and proboscis lengths were significantly larger than those of females.

Table 1. Sexual size dimorphism of adult *Limnoporus rufoscutellatus* (length in mm, means and standard deviations,  $n=10$  for each sex), and coefficients of size variation and their standard deviations (in parentheses). Statistical significance based on  $t$  tests (\*\*\*= $P < 0.001$ ; \*\*= $P < 0.01$ ; NS=not significant at the  $P$ -level 0.05).

Sex	Body	Mesothoracic femur	Pro-boscis
♀♀	15.3±0.8 (5.2±1.16) *** NS	8.0±0.4 (5.0±1.11) *** NS	2.6±0.1 (3.8±0.84) *** **
♂♂	14.1±0.8 (5.7±1.27)	7.8±0.7 (9.0±2.01)	2.4±0.2 (8.3±1.85)

#### 4. Results from nature

##### 4.1. Early summer densities and turnover

Results from the 3 ponds are collated into Table 2. The two sexes were found in equal densities. Total density varied from below 0.1 to 1 strider per metre of shore line with vegetation. On peak days, about one male per metre was counted along the best 20 m stretch in the large pond.

Daily turnover rates of both males (median 80%) and females (70%) were almost equally high in the two small ponds, but significantly lower for the males (45%) in the larger pond (83% for females). Altogether 11 males and 5 females (9 ♂♂ and 1 ♀ in the large pond) were located at the same site on two successive days. No strider kept its site for three successive days.

##### 4.2. Territorial behaviour

Nine of all the 68 males observed in Tvärminne behaved territorially. Territorial males defended a fixed territory within about a 50 cm radius of their site of attachment.

The site of attachment of a territorial male was usually floating vegetation, to which the male was most frequently anchored by a mesothoracic leg. The main reason for the male leaving his territory centre was to chase away alien individuals, which were not necessarily conspecifics. Males even behaved aggressively towards, or tried to mate with, tandem couples of other species. After chasing some males patrolled the pond for a couple of minutes, and then returned to the territory centre. When the territory had become occupied by another male, the new male was forced away by the homing male. When a territorial male encountered another territorial male while patrolling outside his territory, he behaved non-aggressively and escaped if attacked (observed twice in nature and more than ten times in the laboratory).

Encounters among adults of *L. rufoscutellatus* frequently involved signalling by surface waves. When an alien skater approaches a territory, its owner may emit an HF-signal before moving ahead. We observed more than 10 times an approaching male withdraw after receiving an HF-signal emitted by a territorial male. Often an approaching male did not signal before the territory owner had attacked

Table 2. Daily numbers and turnover (medians in parentheses) of *Limnopus rufoscutellatus* males and females in three south Finnish ponds in the period 3.-10.6. (large pond) and 5.-10.6. (small ponds). Length of shore line in metres (shore line with vegetation in parentheses).

	Area m <sup>2</sup>	Shore- line	Daily numbers		Daily turnover	
			♂♂	♀♀	♂♂	♀♀
Large pond	370	75 (60)	7-29	7-30	37-63 (45)	60-92 (83)
Small pond 1	100	37 (27)	1-13 <sup>1</sup>	3-14 <sup>1</sup>	53-82 <sup>1</sup> (80)	60-87 <sup>1</sup> (70)
Small pond 2	70	30 (25)				

<sup>1</sup> Common data for the 2 small ponds.

him, but then he usually signalled and retreated. Male encounters were usually solved rapidly by attack and escape. In nature we only once observed an extended fight which lasted for half a minute. Then both the territorial male and the alien one attacked and retreated several times, after which the alien male withdrew. It seems that the territory owner usually wins the conflict.

Signalling (by both territorial and non-territorial reproductive males) is a means of identifying the sex of the approaching individual. If the latter does not emit back any signal, the male judges (not always correctly, because a male may also refuse to answer; cf. above) that the approacher is a female. The male starts courting by emitting another kind of surface wave. If the female is not receptive, she may advertise the fact with a specific burst of signal waves. A female ready to mate lowers her abdomen, but an unreceptive female raises her body high upon her legs above the water surface (unpublished).

In nature we recorded territories which lasted (and were defended) for several hours, but as a rule they were abandoned by the next day. Then the territorial males moved around in the pond and behaved non-aggressively. The maximum observed duration of a territory was 3 days. This was during a rainy period when the activity of striders was quite low. One territory lasted for 2 days, after which the pond dried up and the striders disappeared (the founding date of the territory remained unknown, however). The shortest observed territory lasted for 15 minutes, and after that the male skated away without any visible reason and did not return within the following one-hour observation bout. However, as the



founding of the territory was not known, its actual duration may have been longer.

Of the 9 territorial males 3 were observed to found new territories elsewhere in the pond within some days after giving up the former one. Before founding a territory, and in between territorial periods, they behaved non-aggressively.

More than half of all male-male encounters within a territory included aggression by territorial males. Males fell into two distinct groups with respect to aggression: aggressive territorial males, and nonaggressive, non-territorial males.

## 5. Discussion

### 5.1. Size and territorial success

Reproductive males of *L. rufoscutellatus* are territorial, while females and diapause males are not. Only a minority of local males at any time defend territories, which, moreover, are fairly temporary. In the laboratory several territories lasted for a week (the maximum run of an experiment), but in nature even a day-long territory seems infrequent. The effect of density on the frequency of territorial males and the persistence of territories is not known. The results are similar to those obtained by Spence & Wilcox (1985) on two Nearctic *Limnopus* species, *L. notabilis* (Drake & Hottes) and *L. dissortis* (Drake & Harris) in nature.

Males usually abandoned their territories without any obvious reason, and we generalise that a resident male on his territory usually wins conflicts with an approaching alien male. The duration of territory occupation and/or recent success in male-male encounters on the territory rather than size-correlated physical strength seems important in explaining the later success of males in defending their territories. Spence & Wilcox (1985) did not find any correlation between the size of the male and his success in territorial contest in the two Nearctic species either.

Our result is similar to that described by Davies (1978) for the butterfly *Pararge aegeria*. It is also in agreement with the theoretical predictions by Maynard Smith & Parker (1976), which make the point that for the outcome of territorial conflict the fighting abilities of the males are irrelevant. They also predict that

escaleted fights should occur only when both contestants 'feel' that they are on their own territory. This conclusion also seems to be valid for *L. rufoscutellatus*, and was probably the reason for ardent fights between territorial and introduced males of the grasshopper *Ligurotettix coquilletti* in experiments by Otte & Joern (1975).

### 5.2. Function of territoriality

The territory is typically about 50 cm in radius, and the male positions himself at the centre. From there he skates towards approaching waterstriders, and frequently emits an HF surface wave signal. The function of signalling in a *Limnopus* male is to solve the sex of the approacher (Wilcox & Spence 1985, Nummelin unpublished). A male is chased away, but females are approached for mating. The function of territoriality in *L. rufoscutellatus* males is supposed to be mating, just as in the Nearctic congeners (see Spence & Wilcox 1985).

The other Finnish Gerrid known to be territorial is *G. najas*. In this species the reproductive female defends territories, and the function is food which should increase female fitness by increased egg production and egg size (Vepsäläinen & Nummelin 1985). But the function of male territoriality in *L. rufoscutellatus* is definitely not food. On the contrary, males often leave their territories temporarily to forage. And in our preliminary laboratory experiments with food concentrated within a patch in the basin the patch was frequented both by non-territorial and territorial males. None of them was seen even to make an attempt to found a territory there. Our results are similar to those obtained by Spence & Wilcox (1985) for the two Nearctic *Limnopus* species in nature. But of course the reason why *L. rufoscutellatus* has not evolved territorial for food is because of its natural environment. There food at any one site is supplied unpredictably in time and no defendable food aggregations are formed (Vepsäläinen 1985).

### 5.3. Evolution of size dimorphism

The female *L. rufoscutellatus* is only slightly larger than the male (a ratio of below

1.1 for several measurements), and thus the species forms the extreme for reduced sexual dimorphism in European Gerrids. The other extreme is found in *G. najas*, where the size ratio between the female and male sexes is exceptionally large. It may not be a mere coincidence that in *G. najas* the female is the territorial sex (Vepsäläinen & Nummelin 1985).

Interestingly enough, the male-territorial *L. notabilis* is the only waterstrider species known to us where the male is even larger than the female (Calabrese 1983). It would therefore seem plausible to explain the pattern of sexual size dimorphism as a consequence of territoriality: large striders would be favoured in territorial contests. But this was clearly not the case either in our, or in Spence & Wilcox's (1985), studies on various *Limnopus* species: success did not correlate with size.

Spence (Spence & Wilcox 1985) has suggested that *dominance* is the key feature in selection for large size, and dominance could be only loosely correlated with the adoption of a mating tactic. The interpretation is supported by the behaviour of *Limnopus* males: in nature they rarely keep territories longer than for a day at a time, after which they switch to another mode of behaviour. The best tactic should depend on the ambient environment, including the density and status of other males and the behaviour of females.

#### 5.4. Alternate mating tactics

Hayashi's (1985) results on the Japanese *Gerris elongatus* (Uhler) indicate that the best tactic may change as a function of developing vegetation (see also Spence & Wilcox 1985 for the two Nearctic *Limnopus* species). Yet another complicating environmental factor was recently found by Spence (1983): a Scelionid wasp (*Tiphodytes gerriphagus*) restricts Gerrid population growth through heavy parasitism. The egg parasitism is density-dependent, and may play an important

role in tipping the balance between female behaviour favouring oviposition in male territories vs. elsewhere. Variation in oviposition tactics by females would then allow an overall mixed male mating strategy (Spence & Wilcox 1985).

Virtually nothing is known about the parasitism of North European Gerrids. But normal densities of breeding *L. rufoscutellatus* seem strikingly low in comparison to sympatric Gerrids (Vepsäläinen 1973) or even to the Nearctic congeners (John Spence, personal communication). The causal relations between the low densities, territoriality and possible parasitism of *L. rufoscutellatus* remain unsolved. However, it is evident that comparative studies on the behavioural ecology of Nearctic and Palearctic *Limnopus* should be encouraged.

Wilcox & Ruckdeschel (1982) have shown that in *G. remigis*, the Nearctic ecological equivalent of *G. najas*, both sexes and the older nymphs are all territorial, both in the reproductive season and during diapause. It is thus clear that no standard *Gerris* territoriality pattern exists. Rather Gerrids offer themselves as a potential group for the study of territoriality as a flexible adaptive strategy in specific ecological situations. Hence, the function of territoriality should be sought in relation to the pattern of the environment. Different environments produce different challenges to individuals and populations, which should be solved by differing strategies, i.e., differing sets of tactics. An important corollary of this idea and the observed frequent switching of *Limnopus* males between different modes of behaviour is that territoriality is not *the* adaptive mating strategy, but only one of two or more alternatives available to the males.

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