

ORIGINAL ARTICLE

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Microhabitat selection and audible sexual signalling in the wolf spider *Hygrolycosa rubrofasciata* (Araneae, Lycosidae)

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Abstract We studied the microhabitat selection and male sexual signalling behaviour in the wolf spider *Hygrolycosa rubrofasciata* (Ohlert). Males strike dry leaves with their abdomen, producing an audible sexual drumming signal, and females use this signal to choose mating partners. In the field we followed male drumming rate and microhabitat selection using both the mark–recapture method and direct observations. In the laboratory we conducted an experiment on male microhabitat and drumming substrate selection. We found that in the field males were not distributed randomly among the habitat; fewer males were found in areas that had high sedge cover, low elevation, and low dry leaf cover. In the laboratory experiment, males spent more time on dry leaf substrate. Drumming rate in the field was positively correlated with dry leaf cover and in the laboratory males clearly preferred dry leaves as drumming substrate. Temperature was positively correlated with male drumming rate, and with male and female mobility. We conclude that in *H. rubrofasciata* male distribution and sexual signalling rate, and thus mating success, are greatly affected by environmental factors. Therefore, males may be sexually selected to make effective use of their signalling habitat by active microhabitat choice.

Key words · Sexual signalling · Courtship drumming · *Hygrolycosa rubrofasciata* · Microhabitat selection · Sexual selection

Introduction

Sexual selection often favours individuals that are efficient in sexual signalling (Andersson 1994). Of the factors that may affect the efficiency of sexual signalling, internal factors, such as individual condition or size (e.g. Johnstone 1995; Crnokrak and Roff 1998), have generated considerable interest among students of sexual selection, but there are fewer studies on external factors, such as effects of temperature and surrounding habitat (Bailey 1991; Andersson 1994). However, it is conceivable that especially in poikilothermic animals environmental factors such as temperature may have a profound effect on signalling efficiency and thus on their mating success.

Sound production by spiders has been noted in 26 families and is known to occur in at least three behavioural contexts: courtship, inter-male aggressions, and defence against predators (Uetz and Stratton 1982). There are reports of several different mechanisms of sound production, but all can be categorised as two distinct classes: stridulation, which is produced by the friction of two body parts, or percussion, which is produced by striking the substrate with legs, pedipalps, or abdomen (Rovner and Barth 1981; Foelix 1982; Uetz and Stratton 1982; Fernandez-Montraveta and Schmitt 1994).

Hygrolycosa rubrofasciata (Ohlert) is a ground-dwelling wolf spider (Lycosidae) with an audible sexual signal. Males produce two distinct types of signals: one during inter-male aggressions (Kotiaho et al. 1997, 1999a) and the other during courtship (Kotiaho et al. 1996; Parri et al. 1997). In this study we focused only on the courtship drumming (hereafter simply drumming). Males produce drumming by striking their abdomen against substrate in rapid bursts. This generates a drumming sound that can be heard about 10 m in distance under field conditions. One drumming consists of 30–40 pulses and lasts about 1 s (Rivero et al. 2000; Kronstedt 1996). Males engage in drumming without the presence of females and an average drumming rate in laboratory is just above one drumming per minute (e.g. Kotiaho et al. 1996; Mappes et al. 1996). However, presence of a fe-

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male increases male drumming rate on average 85% (Mappes et al. 1996).

Males search for females and move relatively long distances around the habitat, whereas females seem only to move very little and short distances (Kotiaho et al. 1999b). While searching, males stop occasionally and engage in drumming. Drumming has been shown to play a very important role in mate choice in this species: females preferentially mate with males that have high drumming rates (Kotiaho et al. 1996, 1998; Parri et al. 1997). Furthermore, despite extensive mating trial observations, we have not observed matings to occur without male drumming (Alatalo et al. 1998).

H. rubrofasciata inhabits mostly moist meadow or bog habitats with moss (*Sphagnum* spp.), hay (Poaceae), or sedge (Cyperaceae) and some deciduous trees and bushes (*Betula* spp. and *Salix* spp.). Areas are characteristically rather open, allowing the snow to melt and the ground to warm up early in the spring. During the spring, wet leaves, dry leaves, and moss patchily dominate the habitat. However, later in the season habitats become covered with dense and rather high vegetation. In southern Finland mating starts soon after snowmelt in mid- to late April and most of the matings are likely to happen within a rather short period from the end of April to the end of May. Each adult male cohort reproduces only during one mating season and males die during or immediately after it. However, we have observed individually marked females to survive until the next mating season.

In this study our objective was to determine the environmental factors affecting male microhabitat selection and sexual signalling during the mating season in the wolf spider *H. rubrofasciata*. In our study we focused on four environmental factors: abundance of dry leaves, the cover of the sedge, elevation of the habitat patches, and temperature. In the laboratory we experimentally tested whether males choose to drum on a particular substrate over others and determined the time spent on different substrate types.

Methods

Microhabitat selection

Microhabitat selection was studied in 1993 on a bog at Sipoo, southern Finland (60°16'N, 25°14'E). We selected an area of 7×7 m where males were drumming actively and divided it into 49 squares of 1×1 m. These squares were further divided into 20×20 cm sections in which three habitat characteristics were measured: elevation of the habitat, abundance of dry leaves, and the cover of sedge. The cover of sedge was the percentage that sedge and a few other plants covered of each section, and the dry leaf cover was the percentage of dry leaf cover in each of the sections. The two variables were ascribed to three categories: 0–33%, 34–66%, and 67–100%. The elevation of the habitat was ascribed to four categories: <10, 10–20, 20–30, and >30 cm from the lowest part of the study area. Mean habitat values for each 1×1 m square were calculated by using values from the 20×20 cm sections.

Within this area we carried out a mark and recapture study between 11 and 13 May 1993. Males were captured with pitfall

traps, marked individually, and released immediately at the capture site. Pitfall traps were checked every hour during the active period of the spiders. Spiders were marked by placing a small dot of paint on the dorsal surface of the prosoma, opisthosoma, or both. Pitfall traps were constructed from a clear plastic sheet (200×150 mm) and two plastic cups (diameter 65 mm). Traps were dug into the ground so that the plastic sheet was between the cups and functioned as a fence that directed spiders towards the cups. Spiders were unable to climb out of the plastic cups. We did not observe any cannibalism or predation in our pitfall traps. Pitfall traps were situated in the centre of each 1×1 m square such that the fence between the cups was alternately oriented north-south and east-west.

In 1994 we conducted another mark and recapture study in a different area (10×10 m) of the same bog. The protocol for the study was as described for 1993. This year we estimated the population size by using Petersen estimate of population size from mark-recapture data ($N=Mn/m$; M is number of marked individuals released from the first sample, n is the number of the individuals in the second sample, m is the number of marked individuals in the second sample, and N is the estimated population size) (Krebs 1989). This estimator is known to overestimate slightly the population sizes (Bailey 1951; Seber 1982; Krebs 1989), but it is useful in giving us an upper estimate of the population size. To increase the confidence of the estimate we calculated the estimate four times by using two successive days (5 and 6 May, 6 and 7 May, 7 and 8 May, and 8 and 9 May) and report the mean and standard deviation as a population size estimate. Females were not included in the estimate because they were too difficult to trap in any great number.

Sexual signalling

Prior to the pitfall study in 1993 we estimated the drumming rate of individual males in the same area. Each 1×1 m square was intensively observed from a close range (<0.5 m) for a period of 5 min and each male drumming was recorded. Seeing the individuals was difficult but males were easily located by their drumming. Observations were repeated on 3 successive sunny and warm days (6–8 May 1993) between 1100 and 1400 hours, when spiders are most active.

At the population level, drumming activity was measured in 1994 between 3 and 9 May and in 1996 between 13 and 25 May. For the measurements in 1994 we divided the study area (10×10 m) into four sections. Population-level drumming activity was estimated by standing in the corner of each section and counting all drums heard within the section for one minute. Measurements were repeated four to six times a day with an interval of 1 h during 7 successive days. In 1996, population-level drumming rate was measured at 1200 hours from six spots separated by 10 m by counting all drumming heard during 2 min. During both years temperature measurements were taken simultaneously with the drumming rate measurements.

Laboratory experiment

We conducted a laboratory experiment on male habitat selection and time allocation among four different habitats in 1996. An arena of 15×10 cm was divided into four sections into which we placed different substrates: wet leaves, dry leaves, moss, and bare soil. These four substrate types were selected because they are the most abundant in our field study sites. Wet leaves were moistened such that they were softer and less crispy than the dry leaves. We collected males randomly from the field in the morning, transported them to the laboratory packed individually in moss-filled small plastic jars, and tested them in the laboratory during the same afternoon. Males were released in the study arena at the crossing of the four habitats. Ten males were observed for 20 min each, one at a time, and the time spent in each habitat was recorded. Also male drumming behaviour in the four different habitats was recorded.

The arena was cleaned after each male and used habitat material was changed for fresh material. The position of the four habitat sections was randomly allocated in the arena for each male.

Results

Habitat selection

During the 1993 pitfall study we captured and marked 112 males of which 77 were recaptured at least once. The mean number of males captured with pitfalls was 0.67 ± 0.71 (SD) per day per square. In 1994 we caught and marked 206 males and 38 females. This corresponds to 0.58 ± 0.46 (SD) males and 0.05 ± 0.10 (SD) females per day captured with pitfalls per 1×1 m square. We recaptured 139 of the males but only 3 of the females at least once. In 1993 recapture rate for males was 68.8% and in 1994 it was 67.5%. Female recapture rate in 1994 was only 7.9%. Population size (males only) estimated from 1994 data by using Petersen index was 2.12 ± 0.27 (SD) males per 1×1 m square (see methods for details of the analysis).

Male distribution within the habitat based on the pitfall captures was not random; males were more aggregated than expected from a random uniform distribution (Kolmogorov–Smirnov test $z=3.47$, $n=49$, $P<0.001$). The three habitat characters were highly correlated and thus a principal component (PC) analysis was performed. Cover of the dry leaves and elevation contributed positively and approximately equally to the loading of the PC1 (0.41 and 0.41, respectively); cover of sedge also loaded positively but less strongly (0.35). On PC2 cover of sedge loaded strongly and positively (1.13) while cover of leaves and elevation loaded less and negatively (-0.42 and -0.55 , respectively).

Male distribution was not related to PC1 but was negatively related to PC2 ($r=0.057$, $n=49$, $P=0.696$ and $r=-0.291$, $n=49$, $P=0.042$, respectively) (Fig. 1). This analysis indicates that there were fewer males in areas with high sedge cover, low elevation, and low dry leaf cover.

Drumming rate

In 1993 we observed on average 2.3 ± 2.0 (SD) drums per minute per square. Repeatability (Lessells and Boag 1987) (CI 95%) of drumming rate between days in a square was 0.41 (0.23_{Lower} , 0.58_{Upper}) (ANOVA: $F_{48,98}=3.06$, $P<0.001$). Drumming rate was strongly positively correlated with PC1 and negatively with PC2 ($r=0.57$, $n=49$, $P<0.001$ and $r=-0.33$, $n=49$, $P=0.020$, respectively) (Fig. 2). This analysis indicates that dry leaf cover and elevation were positively related and cover of sedge negatively related to drumming rate.

At the population level, drumming rate correlated positively with temperature both in 1994 and 1996 ($r=0.71$, $n=136$, $P<0.001$ and $r=0.86$, $n=62$, $P<0.001$, re-

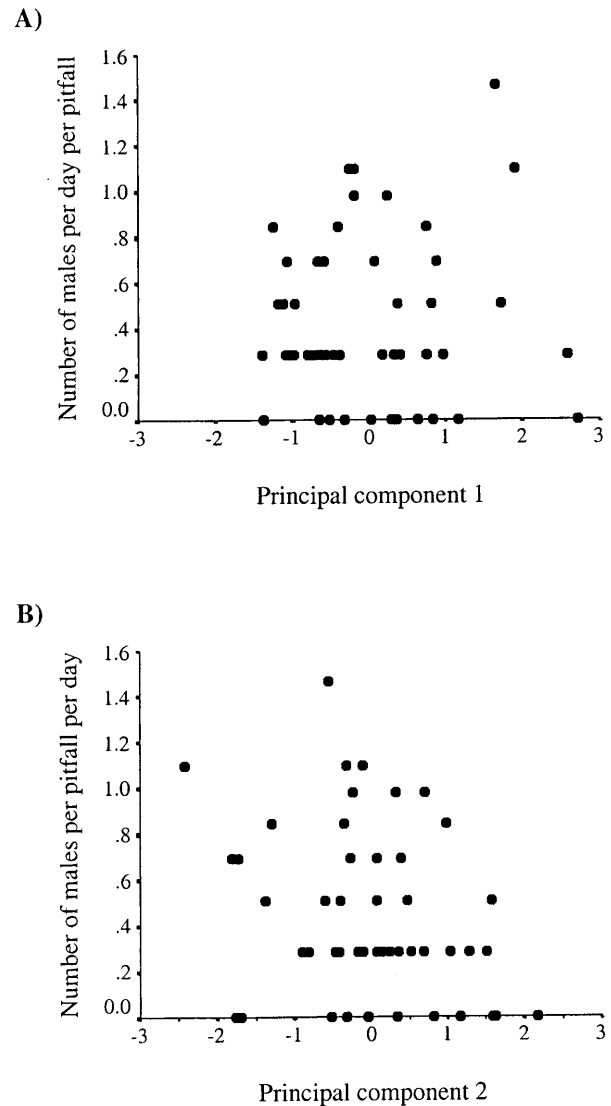


Fig. 1 Correlation between number of males captured in pitfalls per day and **A** the first principal component and **B** the second principal component of the habitat variables

spectively) (Fig. 3). Temperature was also positively correlated with the number of males and females captured with the pitfalls in 1994 [$r=0.85$, $n=7$ (days), $P=0.016$ and $r=0.87$, $n=7$ (days), $P=0.010$, respectively].

Laboratory experiment

There were differences in male habitat use between the four habitat sections (Friedman ANOVA, $\chi^2=10.32$, $df=3$, $n=10$, $P=0.016$). Males spent significantly more time on dry leaves than on other substrates but there were no differences between other substrates (Fig. 4). The difference between the substrates used in drumming was even more pronounced (Friedman ANOVA, $\chi^2=28.71$, $df=3$, $n=10$, $P<<0.001$). There was only a single drumming bout on soil habitat; all the other drum-

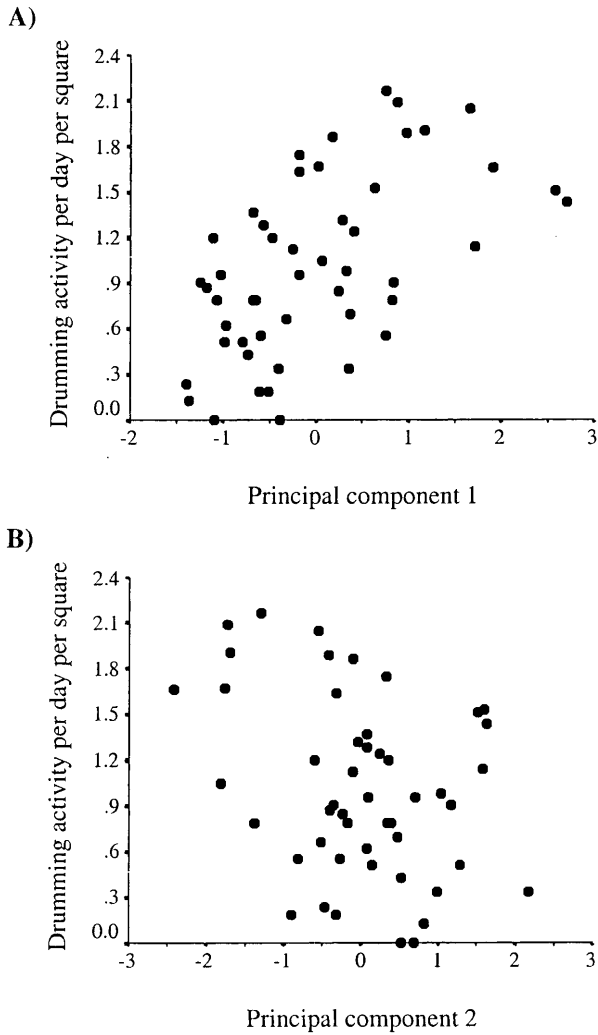


Fig. 2 Correlation between drumming rate per square per minute and **A** the first principal component and **B** the second principal component of the habitat variables

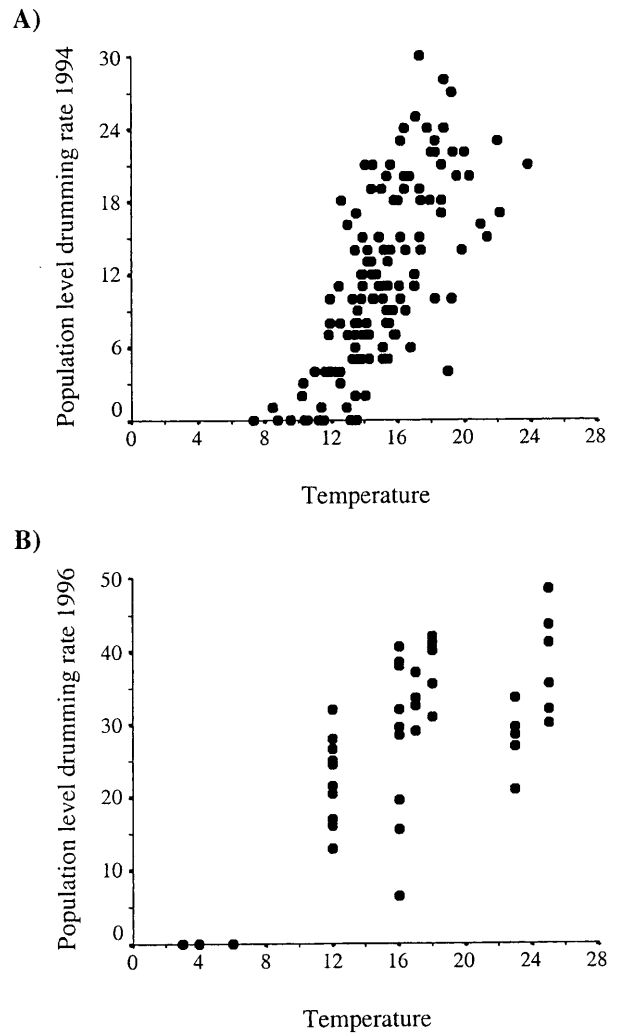


Fig. 3 Correlation between population level drumming rate per minute and temperature in **A** 1994 and **B** 1996

ming bouts were on dry leaves. Overall drumming rate in the laboratory experiment was 0.47 ± 0.35 (SD) per minute.

Discussion

The main findings of our study were that males were not randomly distributed throughout the habitat and that the environmental characteristics had a strong influence on male sexual drumming rate. There were fewer males in areas that had high sedge cover, low elevation, and low dry leaf cover, and drumming rate was highest in areas that were elevated from the surrounding habitat, had abundant dry leaf cover, and low sedge cover. These results indicate that males avoid areas with high sedge cover and low elevation, and that they actively select the areas where they carry out drumming. This conclusion is further supported by our laboratory experiment, in which

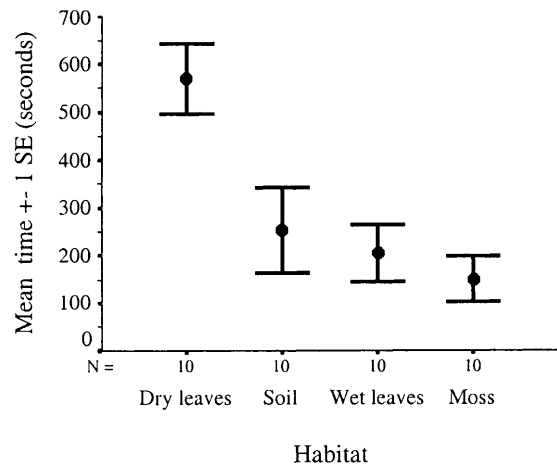


Fig. 4 Mean time ± SE that males spent in different habitats in the laboratory experiment

males spent the most time on dry leaf habitat and chose to drum almost exclusively on dry leaves.

It has been suggested that the physical properties of sound propagation may be important in shaping animal sound communication systems (e.g. Bennet-Clark 1989; Bailey 1991). Generally, sound waves spread spherically from their place of origin. In natural settings, however, sound waves will be partly reflected and partly absorbed by the surrounding structures. Reflection and absorption of sound waves make them less coherent, reduce the signals' clarity, and generally result in faster attenuation of the sound (Bailey 1991). Because the nature of the surrounding structures determines the rate of sound attenuation, it is likely that animals have evolved morphological or behavioural adaptations that reduce this attenuation and improve their sound propagation. Indeed, many animals have evolved morphological structures that make them acoustically very efficient senders (e.g. Bailey 1978; Uetz and Stratton 1982; Aiken 1985) and some shape their surroundings such as to improve their sound propagation (e.g. Bennet-Clark 1987; Bailey 1991).

We suggest that the observed non-random distribution of *H. rubrofasciata* males in the field may result from males distributing themselves favourably in regards to signal propagation. Males were found to be drumming most actively in areas with low sedge cover and relatively high elevation. Both low sedge cover and relatively high elevation are likely to reduce the reflection and absorption and thus attenuation of sound by reducing habitat structures interfering with the sound waves, thereby improving sound propagation.

There was a strong positive correlation between temperature and drumming rate. In addition, there was a threshold temperature of about 10 °C for males to start drumming and even a 1–2 ° increase in temperature rapidly increased the drumming rate of males (Fig. 3). At the time of the peak mating season in late April and early May, the ground in our study sites is still frozen after the winter and the temperature falls below zero during most nights. Given that spiders are poikilothermic (Foelix 1982) and the observation that there exists a threshold temperature for drumming, it is very likely that temperature is a limiting factor for mating activities. Males that actively choose their microhabitat, avoiding shaded and thus cold areas as well as low elevation and high sedge cover, may be able to increase their drumming rate and drum for longer periods of the day, thus considerably increasing their probability of mating (Kotiaho et al. 1996; Parri et al. 1997). Mobility of the males also has a great influence on their mate finding and mating probability (Kotiaho et al. 1998). We found a positive correlation between temperature and number of males captured in pitfalls. Number of males captured in pitfalls may be taken as a direct estimate of male mobility, and therefore, it seems that in addition to having an effect on drumming rate, choosing a warmer microhabitat may increase the mating success of the males through increased mobility.

In conclusion, the pursuit of increased mating success requires effective sexual signalling. In *H. rubrofasciata*

this may be partly obtained through active microhabitat choice; increased signalling rate with increasing temperature and reduced environmental sound attenuation with reduced surrounding structures are both likely to affect the microhabitat selection. Our results show that even small-scale environmental factors had a great effect on males' sexual signalling rate and mate-searching activity and consequently also their reproductive success. Therefore, it seems that males may be sexually selected to exercise active microhabitat choice to optimise their environmental conditions for sexual signalling.

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