

Laboratory temperature preferences of the wolf spider *Pardosa riparia* (Araneae: Lycosidae)

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Summary

Many lycosid species have particular temperature preferences that may differ between sexes and the breeding status of the females. In a laboratory experiment using a temperature gradient apparatus, 31 males, 31 females before egg-laying and 31 females with an egg-sac of the wolf spider *Pardosa riparia* (C. L. Koch, 1833), were tested to determine their preferred temperature. We found no difference between these three groups with respect to their temperature preference. We determined the optimal temperature of *P. riparia* to be between 35°C and 42°C. In its natural habitat at 1960 m a.s.l. the preference of *P. riparia* for high temperatures compensates for the short snow-free season.

Introduction

Temperature plays a major role in different aspects of a spider's life, e.g. in habitat choice (Wise, 1993), web

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building (Barghusen *et al.*, 1997), development and survival (Li, 2002; Li & Jackson, 1996), copulation duration (Costa & Sotelo, 1984) and escape behaviour (Cobb, 1994). In a field study at the Swiss alpine timberline, we observed that the dominant species, *Pardosa riparia* (C. L. Koch, 1833), a free-hunting wolf spider (Lycosidae), shows a particular distribution pattern. It prefers open sites such as meadows and dwarf shrub heath and avoids the immediate surroundings of the tree trunks (Frick *et al.*, 2007). This could mean that the habitat choices of this species are the result of thermal preferences. Laboratory studies have shown that many lycosid species have distinct thermal preferences (Hackman, 1957; Almquist, 1970; Hallander, 1970; Humphreys, 1987) and that there are even differences between males, females without and females with an egg-sac (Sevacherian & Lowrie, 1972; Humphreys, 1987). Therefore, we tested males, females before egg-laying and females with an egg-sac of *P. riparia* for their temperature preferences.

Material and methods

We collected 93 specimens (31 males [M], 31 females before egg laying [F] and 31 females with an egg-sac [FE]) of *P. riparia* at the timberline (1960 m a.s.l.) on Alp Flix (Switzerland, Grisons, Fig. 1). Sixty-five specimens were collected on 14 June 2004 (31 M, 30 F and 4 FE) and tested. Another 28 specimens were collected on 4 July 2004 (1 F and 27 FE), and tested. Spiders were kept in the laboratory for one week in separate plastic boxes, supplied with drinking water and fed daily before testing.

We used three equally illuminated (approx. 350 lux) circular temperature-gradient apparatuses, each covered by a transparent plexiglass sheet, forming a circular test chamber of 6.5 cm width, 5.0 cm depth and *c.* 185 cm



Fig. 1: Sampling site. Specimens were collected in the meadow and the dwarf shrub heath.

internal perimeter (Fig. 2). The relative humidity was approximately 50%.

We defined 16 equally dimensioned sections in the test chamber: H above the heater, C above the cooler, 7 sections on the left, and 7 sections on the right side (Fig. 2). The test chamber was heated to an average temperature of 54.6°C at one side (section H) and cooled to 17.1°C on average at the opposite side (section C), resulting in a linear gradient on both sides of the test chamber. During the tests, the temperatures were measured with permanently installed thermometers below sections H, C, and 2, 4 and 6 on the left side, and below section 4 on the right side as a control (Fig. 2), and the means were determined. The mean temperatures of all other sections were estimated (Fig. 3).

Each spider was used singly and only once and was released into one random section of the test chamber. After five minutes of acclimatisation, we recorded the current position (section) every two minutes for a period of 40 minutes. After every experiment we cleaned the test chamber with ethanol to ensure that no pheromones could influence the behaviour of the next spider tested.

We tested whether the spiders spent more time in the left or the right section with a Kruskal–Wallis test, and found no differences for any of the three groups (M: $p=0.146$; F: $p=0.505$; FE: $p=0.592$). Therefore, the results for the corresponding sections of the left and right sides of all apparatuses were pooled.

Then we calculated the mean temperature chosen by every single specimen by multiplying the number of

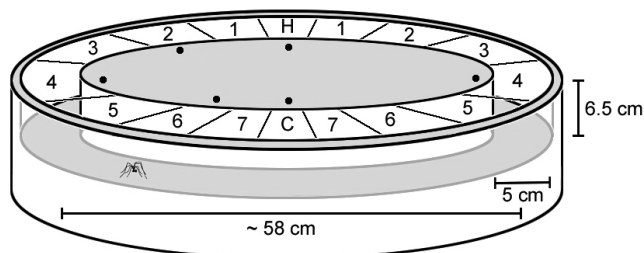


Fig. 2: Model of the temperature-gradient apparatus used. H and C are the sections with an underlying heater or cooler respectively and 1–7 mark the sections in between. Thermometers are marked with black dots.

times a specimen was noted at a certain section by the mean temperature of that particular section, summing the resulting values and dividing by 20, the total number of records for each test. A Kolmogorov–Smirnov test showed that our data were non-normally distributed. We compared the resulting 31 means for each group using a Kruskal–Wallis test. We used SPSS Version 13.0 (SPSS for Windows, Rel. 11.5.0. 2002. Chicago: SPSS Inc.) for all statistical analyses and SigmaPlot Version 9.0 (SigmaPlot for Windows, 2004. Systat Software Inc.) for the graphics.

We utilised weather data from Radons (1870 m a.s.l.; situated on the other side of the valley from Alp Flix) to compute the temperatures for a natural habitat of *P. riparia*. The temperature was measured every hour (in shade, 2 m above ground) during the year 2003, and we calculated the mean temperatures for each week (Fig. 5).

We extracted the phenological data (Fig. 5) from another analysis conducted in 2003–2004 (Frick *et al.*, 2006). In this study, we sampled from mid-May 2003 until mid-May 2004. The snow-free time lasted from mid-May to the end of October. We included only those specimens that were captured in pitfall traps at the location where we collected specimens for this experiment.

Results

Most specimens moved around the whole test chamber before they spent a longer time in certain sections. After a short acclimatisation period with high activity, we observed three types of behaviour during the tests. Some specimens stayed in a certain section or moved only a few cm, some ran in circles for most of the time, while most specimens ran around, and then spent some time in a certain section, which they left again and later chose a section with the same or similar temperature. This could happen several times during the test.

We found no significant differences in the median temperature preferences between males, females without

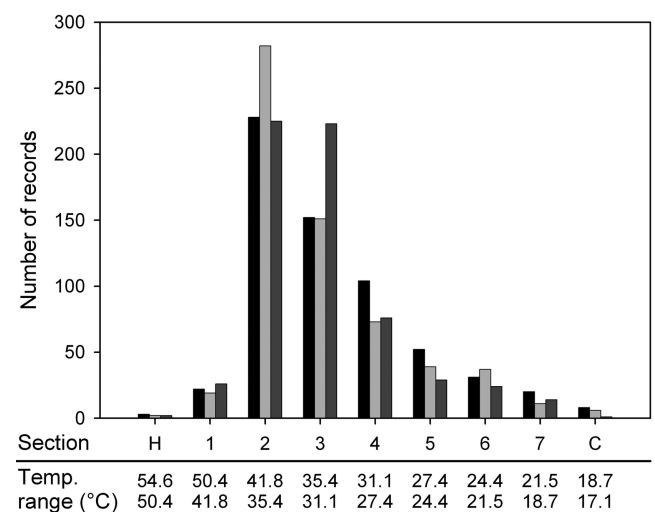


Fig. 3: Number of records per section and group. The lower and upper temperature limit (in °C) of each section is given. From left to right: males (black), females before egg-laying (grey), and females with an egg-sac (dark grey).

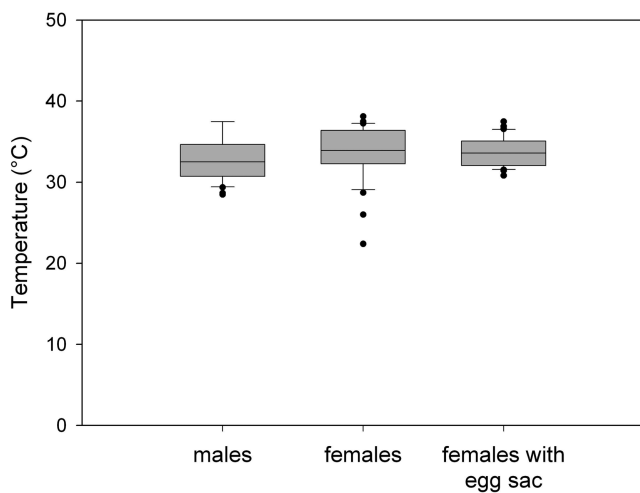


Fig. 4: Preferred temperatures of males, females without and with an egg-sac. Indicated are the median (black line within the grey box), the lower and upper quartiles (sections of the grey box), the lower and upper deciles (lines) and the outliers (black dots).

and females with an egg-sac (χ^2 test, $p=0.160$, Fig. 4). The median temperature was highest for the females without an egg-sac (33.9°C), followed by the females with an egg-sac (33.6°C) and the males (32.5°C).

However, the number of records per section and group showed slight differences (Fig. 3). Males and females without an egg-sac showed a marked peak in section 2, i.e. at an average temperature of 37.5°C (range from 35.4–41.8°C), while females with an egg-sac preferred a broader range with an equal number of records in sections 2 and 3 (range from 31.1–41.8°C, Fig. 3).

Discussion

The preferred temperature of *P. riparia* (based on the numbers of records in a particular section, Fig. 3) was between 31.1°C and 41.8°C. These are rather high temperatures for males and females. It considerably exceeds the optimal temperature for egg development as measured for other lycosids (c. 30°C; Humphreys, 1987). Our observed median temperatures are also slightly higher than that optimal temperature.

Possibly, this high value represents the thermal preference only under laboratory conditions where natural insolation is lacking. Humphreys (1977) stressed that it is difficult to use laboratory data to predict events in the field, because only a few variables are normally considered in the laboratory. Also, the combination of different parameters such as temperature, humidity, insolation, exposure or availability of hiding places are not taken into account although they may influence thermal preferences. Thus our results show only the optimal temperature under our laboratory conditions.

Females with an egg-sac showed a roughly equal preference for two sections in the temperature gradient apparatus, i.e. from 31.1–41.8°C (Fig. 3). This wide range of preferred temperature could be explained by changing temperature requirements of the developing eggs during the period of egg-sac carrying. Thermal optima of lycosid females carrying an egg-sac may be

higher (Nørgaard, 1951; Sevacherian & Lowrie, 1972), lower (Humphreys, 1978), or equal (Nørgaard, 1951; Vlijm *et al.*, 1963) to those of females without an egg-sac. We assumed that females with an egg-sac should have at least a slightly higher temperature preference to accelerate the development of their young. However, Li & Jackson (1996) noted that the rearing of lycosids at very high temperatures (i.e. close to their lethal temperature) leads to considerably retarded development.

The phenological data (Fig. 5) show that *P. riparia* is a stenochronous species which matures and reproduces between mid-May and late July. Specimens overwinter as immature instars, as with most other Holarctic *Pardosa* species (Kiss & Samu, 2002). In spring, longer days and rising temperatures allow the completion of development (late April and mid-May at our study site). Egg sacs appear in late June and early July, spiderlings in late July and early August (Frick *et al.*, 2006). The temperature change in autumn can induce quiescence (Schaefer, 1987), which occurs in late August/early September at our sampling site. Because the warm period on Alp Flix is relatively short and spiders have little time for development or for accumulating nutrients, a high level of activity is required. This might explain the unusually high thermal preferences of *P. riparia*. In addition, the life cycle of *P. riparia* at high altitudes allows spiderlings to use the hottest period of the year for their initial development (Fig. 5). The temperature data shown in Fig. 5 may not represent the real ambient temperatures where we collected the specimens for our tests. Because of shading from the nearby mountains, our sampling area has shorter periods of daylight than the weather station. Furthermore, the temperatures were measured at 2 m above ground level. Therefore, the temperatures shown in Fig. 5 may be lower than at ground level at our sampling site.

Li & Jackson (1996) suggest that species select appropriate seasons in the year to increase their survival and rate of development. Fast development under high

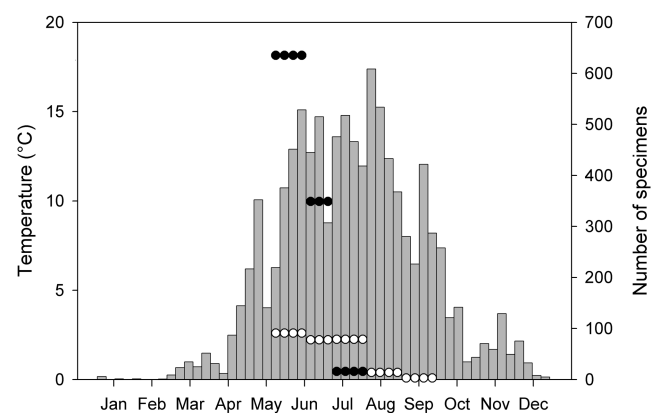


Fig. 5: Comparison of numbers of specimens of *P. riparia* caught in pitfall traps with temperature values from a neighbouring valley. Shown are temperatures (mean temperature for each week in °C, grey bars, left axis) and numbers of males (black dots, right axis) and females (white dots, right axis). A group of three or four dots in a row represent the pooled data for one sampling month (e.g. 635 male specimens between mid-May and mid-June).

temperatures may indicate an adaptation to the warm season (Li & Jackson, 1996). Therefore, we may conclude that *P. riparia* prefers high temperatures, at least at these altitudes, to compensate for the short snow-free period.

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