

The wolf spider *Pardosa alacris* (Araneae, Lycosidae): the courtship display of this and related species and pheromone communication

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Abstract. At first the courtship behaviour of *Pardosa lugubris* (Walckenaer, 1802), morphological polymorphism indicating different species, and *Pardosa alacris* (C. L. Koch, 1833), a closely related species, were videorecorded and analysed. Two distinct types of courtship behaviour in *P. lugubris* quite different from the one of *P. alacris* were revealed. All of them are described in detail in this paper. In the second experiment it was shown that the female can mate a significantly longer time after the last moult than the male can. Finally, a new method for measuring the quantity of the specific male reaction to a dragline is described. By this method the difference between the male reaction to male and female draglines was demonstrated and tried to characterise chemically the presumed female pheromone by evaluation of the male reaction to female draglines washed in a series of solvents.

INTRODUCTION

The wolf spider *Pardosa alacris* occurs regularly in great numbers in deciduous forests on the dead leaf litter. It was until lately considered to belong to the species *P. lugubris* with similar environmental requirements. But Wunderlich (1984) separated, by a difference in the cymbium colour, from *P. lugubris* the species *P. pseudolugubris*, that Kronstedt (1992) documented to be a junior synonym of the name *P. alacris* (Koch, 1833). In addition Töpfer-Hofmann and von Helversen (1990) suggested a separation of another two species from original *P. lugubris* because of morphological characters on the male palp. Besides they mentioned also some differences in the male's courtship display. In the first part of this paper the courtship displays of *P. alacris* and the next two types of males of *P. lugubris* (in this paper indicated as species A and B)¹ occurring on Czech territory are described in detail. The fourth type of male suggested by Töpfer-Hofmann and von Helversen (1990) does not occur in the Czech Republic.

In preliminary experiments I investigated the time between the last moult and sexual maturity, both for males and females of *P. alacris*. The results are presented in the second part of the paper.

¹ Species A and B are *P. "saltans"* and *P. "lugubris s. str."* sensu Töpfer-Hofman and von Helversen (1990).

In spiders the problem of pheromones has been elaborated only a little. As far as I know, the only identification of a spider pheromone was performed by Schulz and Toft (1993), other papers confined themselves to the description of the male responses to drag-lines, left by a spider while walking, washed by solvents. In some spider species the pheromone could be dissolved in polar solvents (e.g. water, isopropanol) but not in nonpolar solvents like hexane (Pollard et al., 1986), in other species the solubility was just the opposite (Lisotte & Rovner, 1989). The male of a lycosid spider, that touched a conspecific female dragline, follows it towards the female with specific movements described like trail-following behaviour, e.g. by Tietjen and Rovner (1980). He walks along the line alternately touching it with palps and jerking the first pair of legs rapidly. The last part of this paper includes evidence of the presence of a pheromone on the female dragline and an attempt to characterise chemically this pheromone in *Pardosa alacris*.

MATERIAL AND METHODS

Spiders

The spiders were collected at early spring, just when they started adult moulting. They were caged in glass vials closed by wet cotton-wool, and fed with adult moths *Ephesia kuehniella*. They had a day of the same length as outdoors and temperatures from about 22 to 26°C. All experiments were carried out in similar conditions.

The courtship display

The behaviour of the spiders was observed in boxes of Plexiglas (about 30 x 20 cm) with the bottom covered by dry oak leaves for imitation of the natural environment. It was videorecorded in petri dishes with white paper beneath using S-VHS camera. The width of the spider was about 20 to 25% of the width of screen. The positions of spiders during courtship display were captured by Screen Machine II (by FAST electronic GmbH) using full frame (736 x 560 pixels). Following the axis of the palps and leg in the pictures were drawn courses of movements during phases using CorelDRAW! (by Corel Corporation), because the outline of the spiders was rather indistinct. It was not possible to determine the borders of the palp segments so the drawings consists of only two sections, which are in the descriptions of the courtship displays called proximal and distal parts.

The period of sexual maturity

By the period of sexual maturity I mean the time, in which the spider is ready to mate after the last moult. In the male it represents the time before he begins the courtship display when presented a female, in the female the time before she mates with the first male.

During the experiments designed to test male and female mating readiness, both mates were placed together in petri dishes for ten minutes. For each of the tested spiders four such experiments per day were performed. Because both the controls of moulting time and the mating experiments were performed once a day, the results were simplified by considering only the difference between time, when the spider was found moulted, and time of experiment, where the spider manifested his sexual maturity.

The pheromones

Following method was used to evaluate male reaction to a dragline. It provides not only the information of if the male reacts but also the quantity of his reaction. By a glass stick of hair diameter I collected the dragline left by a spider in a petri dish, where it had been kept for about a day. The dragline was easily found especially between a piece of wet cotton-wool and the bottom. The stick with wound line was placed in a clean petri dish, on the periphery to be crossed by the male. When the male touched the stick he either did not respond to it, or he showed the trail-following behaviour, which means that he walked along the glass stick with the dragline there and back as described formerly. This behaviour could last from only a moment to several seconds.

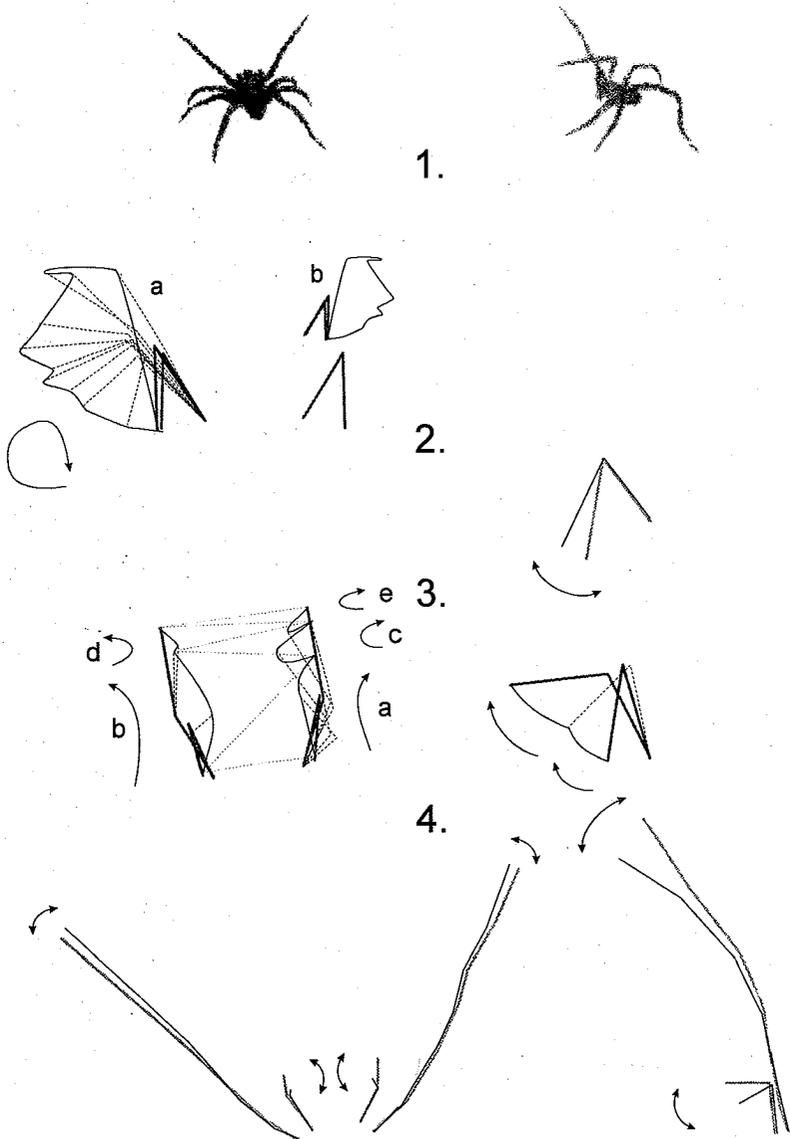
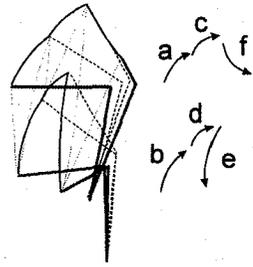
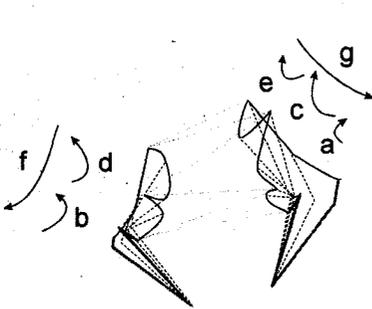
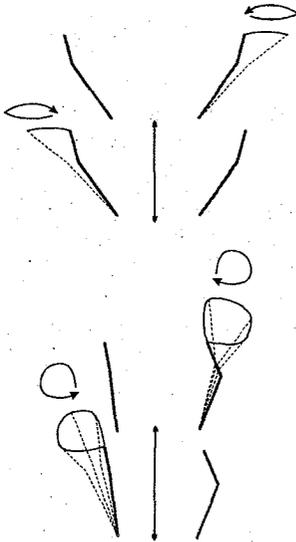


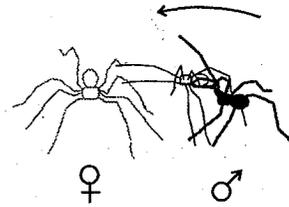
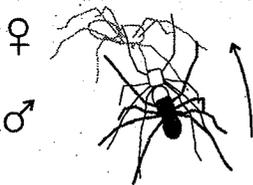
Fig. 1. The courtship display of *Pardosa alacris* (on pages 176–177). The drawings show positions of palps or first pair of legs viewed from behind and from left. In 1st, 3rd and 5th phases are used grey lines for initial and finale position of palps and dashed lines for selected positions of palps from which was constructed the solid line indicating the path of the tip of palps. The outlines of the spiders at the end illustrate the male leaning towards the female. Greyscale pictures at the beginning demonstrate positions of the male from which the drawings were made.



6.a



6.b



I considered it a reaction when the male stopped and followed a little of the dragline. The magnitude of male reaction to the stick with dragline was then expressed by the ratio a/b , where a is the number of the male's crossings of the stick when showing the trail-following behaviour and b is the number of all males' crossings of the stick.

First the difference between male and female dragline was determined. In these experiments glass sticks with both male and female dragline were placed together in a petri dish and male reaction to them was compared. Three males and three females were used, each male tested with each female six times.

Next I tried to characterise the pheromone by male reaction to the female drag-line washed in polar and nonpolar solvents. I used four solvents ranging from nonpolar hexane and ethylacetate, less polar ethanol to strongly polar water. The glass stick with wound female dragline was washed approximately 24 hours in 0.4 ml of solvent and then tested as described above. An unwashed stick with female dragline was used as a control. Four males per one washed stick were used and ten sticks of each type were tested.

RESULTS AND DISCUSSION

The courtship display

Both *Pardosa alacris* and species A males showed a courtship display with their first pair of legs raised. Only males of species B mated with conspecific females without any evident courtship display.

The courtship displays of *Pardosa alacris* I divided into six phases (Fig. 1). The time scale of the display is illustrated on Fig. 2. **The 1st phase** begins with the first pair of legs raised while the male waves his palps one after another. The palps both starts and stops in lower position, i.e. proximal part rather horizontal, distal vertical. **During the 2nd phase** the palps are shaken forwards and backwards. The amplitude gradually increases, from indistinct at the beginning. Intervals between the shakes are irregular and vary between 0.2 and 1 s. **The 3rd phase:** The palps are in succession waved in two or three steps to an upper position where the proximal part is almost vertical and distal horizontal. Then, **in the 4th phase**, the palps are shaken similarly as during the second

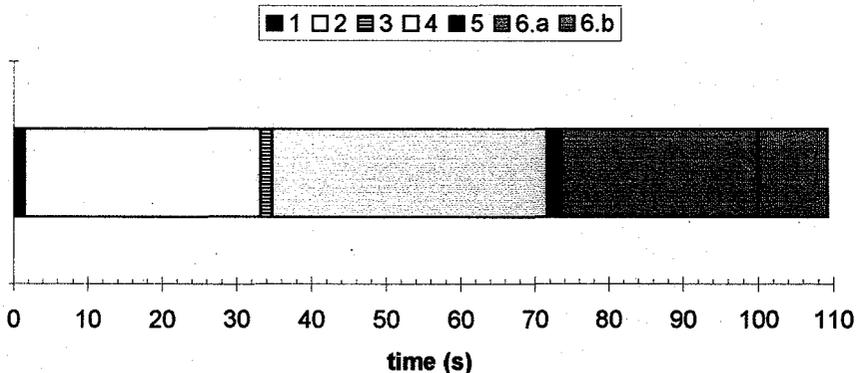


Fig. 2. The course of the courtship display of *Pardosa alacris* combined of average lengths of the phases.

phase, but in an upper position, with synchronous shaking of the first pair of legs. Here the shakes are somewhat grouped (Fig. 3, left). During this phase the male gradually lowers the palps and finally the cheliceres also close and open. **The 5th phase:** The palps are in succession, in several steps, waved up and then laterally. At the beginning of **the 6th phase** the palps are jerking one after another outwards. Later the jerks become circular, the shift being often unclear. The first stage can be called 6.a, the second 6.b. Along with the palps the first pair of legs are jerked one leg towards another and back while the abdomen is jerking up. The spider is gradually leaning towards the female and the frequency of jerks grows. (Fig. 3, right). If the female stays during the whole display motionless, as well as when the leaning male touches her, the mating follows.

The courtship display of species A can be divided also into six phases that are quite different from *P. alacris*. (Figs 4, 5). **The 1st phase:** The first pair of legs is also raised, and the wave of palps is also similar to *P. alacris*, but first both palps wave together and they stop in an upper position. **The 2nd phase:** Some time after the first phase starts the synchronous jerks of palps and first legs up and down with intervals from 0.4 to 0.5 s. Along with it the male moves its whole body. The palps are gradually lowered and near the end the cheliceres also start jerking. It finishes in **the 3rd phase**, during which the palps are raised. Those two phases are repeated two to four times. Then, after several seconds, the palps are lowered during **the 4th phase**, while the cheliceres opened in several steps. After the next pause the male in **the 5th phase** jerks his palps up and down, the raised legs jerking opposite. As during the 2nd phase the cheliceres are jerking. The frequency of the movements is now approximately three times per second, it increases a little and suddenly the male very quickly moves his palps up and down, then puts one of his palps outward and from this direction runs in a semicircle towards the female standing in front of him (the whole is **the phase 6**). As in *P. alacris*, if the female remains motionless during the courtship display and at his run to her too, mating follows. In this courtship display the beginnings of the 2nd and 5th phase are more apparent than in *P. alacris* of the 2nd and 4th phase, so it is considered to be here pauses between phases.

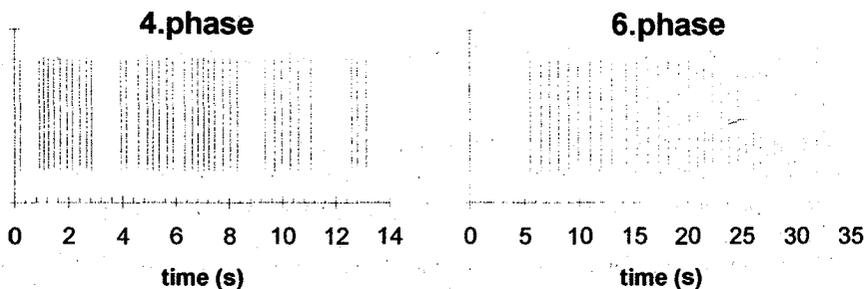


Fig. 3. The course of the 4th and 6th phases of the courtship display of *Pardosa alacris*. Each of the vertical lines indicates one shake of palp.

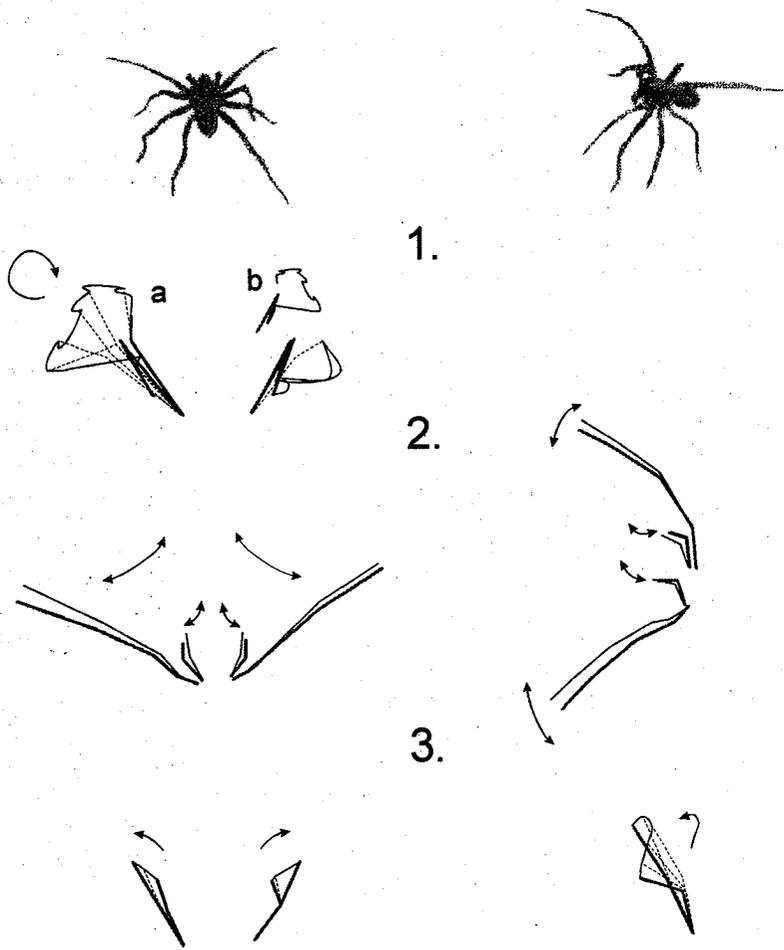


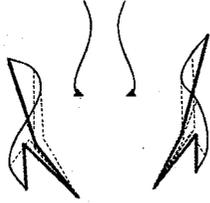
Fig. 4. The courtship display of species A (on pages 180–181). The system of the drawings is similar as in Fig. 1.

The male of species B tries to mount the female in a combat lasting for several seconds. As soon as the male succeeds to mount her, the female remains quiet.

The evident dissimilarity of the courtship displays implies that the males belong to different species.

Three authors investigated the courtship display in *Pardosa lugubris* before the revelation of polymorphism in this species. Vlijm (1966) described, but rather schematically, similar courtship display as described in this paper for *P. alacris*. Only at the end of it he observed a fast run towards the female. Hallander (1967) showed

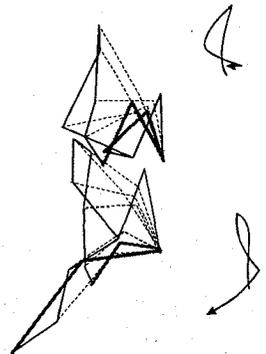
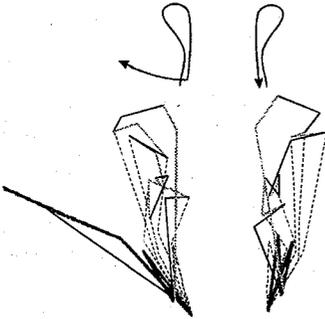
4.



5.



6.



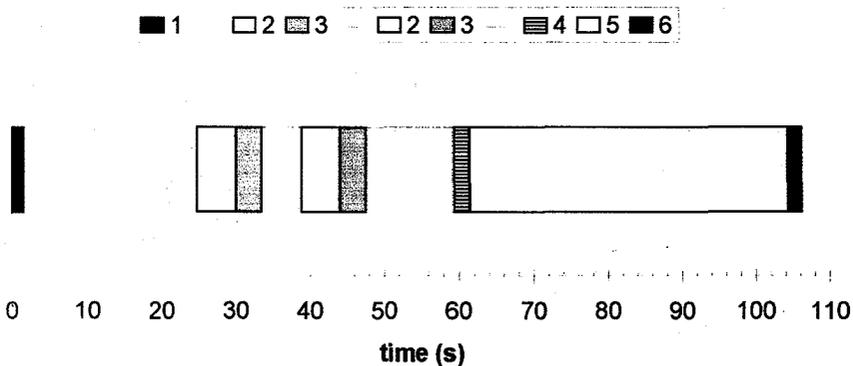


Fig. 5. The course of the courtship display of species A combined of average lengths of the phases. There are presupposed only two repetitions of phase 2 and 3.

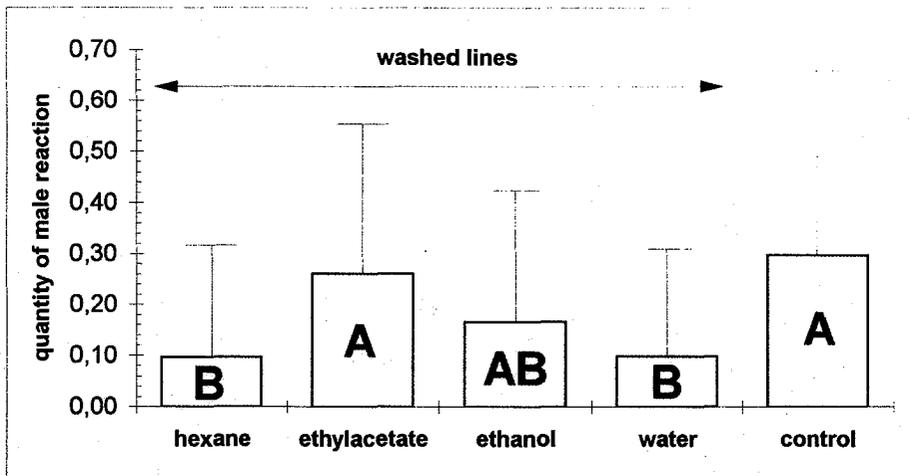


Fig. 6. Reaction of male of *Pardosa alacris* to washed female dragline; A, AB, B—results of Duncan's multiple range test at 5% significance level; control—unwashed female dragline.

courtship display, the beginning of which is similar to the 1st and 2nd phase described here for species A, but the rest is different. The third is Bristowe and Locket (1926) but I unfortunately do not have it.

The period of sexual maturity

The average length of the period in *Pardosa alacris* was significantly shorter in males (2.7 days, S.D. 0.92) than in females (8.3 days, S.D. 4.97) ($F = 17.41$; $P < 0.001$, $N = 15$).

The pheromones

The difference between reaction to the male and female dragline in *Pardosa alacris* is distinct: the average ratio for male was 0.01 (S.D. 0.04) whereas for female 0.54 (S.D. 0.36) ($F = 113.33$; $P < 0.001$; $N = 54$).

Male reaction to female dragline washed in water and hexane is significantly lower than to dragline washed in ethylacetate and to unwashed female dragline (Fig. 6; Duncan's multiple range test at 5% significance level) ($N = 40$, the values are: hexane 0.10, S.D. 0.22; ethylacetate 0.26, S.D. 0.29; ethanol 0.17, S.D. 0.26; water 0.10, S.D. 0.21; control 0.30, S.D. 0.36)

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REFERENCES

- BRISTOWE E. S. & LOCKET G. H. 1926: The courtship display of British lycosid spiders and its probable significance. *Proc. Zool. Soc.* **22**: 317–347.
- HALLANDER H. 1967: Courtship display and habitat selection in the wolf spider *Pardosa chelata* (O. F. Müller). *Oikos* **18**: 145–150.
- KOCH C. L. 1833: Arachniden. In Herrich-Schäffer G. W. (ed.): *Faunae insectorum Germaniae initia*. Heft 120, Regensburg (Fr. Pustet).
- KRONESTEDT T. 1992: The identity of *Pardosa alacris* (C. L. Koch 1833) (Arachnida: Araneae: Lycosidae). *Seckenbergiana biol.* **72**: 179–182.
- LISOTTE R. & ROVNER J. S. 1989: Water-resistant sex pheromones in lycosid spiders from a tropical wet forest. *The Journal of Arachnology* **17**: 123.
- POLLARD S. D., MACNAB A. M. & JACKSON R. R. 1986: Communication with chemicals: pheromones and spiders. In Nentwig W. (ed.): *Ecophysiology of spiders*. Heidelberg, Springer-Verlag.
- SCHULZ S. & TOFT S. 1993: Identification of a sex pheromone from a spider. *Science* **260**: 1635–1637.
- TJETJEN W. J. & ROVNER J. S. 1980: Trail-following behaviour in two species of wolf spiders: sensory and ethoecological concomitants. *Anim. Behav.* **28**: 735–741
- TÖFFER-HOFMANN G. & VON HELVERSEN O. 1990: Four species of the *Pardosa lugubris* group in Central Europe (Araneae, Lycosidae)—a preliminary report. *Bull. Soc. europ. Arachnol.* **1**: 349–352.
- VLIJM L. & DIJKSTRA H. 1966: Comparative research of the courtship-behaviour in the genus *Pardosa* (Arach., Araneae) I. Some remarks about the courtship display of *P. amentata*, *P. hortensis*, *P. nigriceps* and *P. lugubris*. *Seckenbergiana biol.* **47**: 51–55.
- WUNDERLICH J. 1984: Beschreibung der Wolfspinne *Pardosa pseudolugubris* n. sp. und Revision der *Pardosa amentata*-Gruppe, zugleich ein Beitrag der innerartlichen Variabilität bei Spinnen (Arachnida, Araneae, Lycosidae). *Neue Entomologische Nachrichten* **10**: 11–15.