

## **Quantitative analyses of male courtship behaviour in *Pholcus phalangioides* (Fuesslin, 1775) (Araneae, Pholcidae)**

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### **Summary**

Behaviour preliminary to copulation is described in *Pholcus phalangioides* (Fuesslin, 1775). Courtship may be characterized as consisting of four elements: abdominal vibrations, tapping female's web, web jerking, and tapping female's legs. The possible functions of the courtship elements described and their intrapopulation variation are discussed. Some information on copulation duration is presented.

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### **Introduction**

Females of *Pholcus phalangioides* (Fuesslin, 1775) seem to make nearly all the parental investment (produce larger gametes, look after egg sacs); males probably provide nothing more than sperm (pers. obs.). In other animals, females are often choosy, preferring certain morphological features (also behavioural ones) possessed by their mates (Anderson, 1994). Male behaviour during courtship may be a sign of his condition. It also functions to suppress the female's prey-catching instincts (Witt & Rovner, 1982).

Numerous studies have contributed to our understanding of reproduction biology in *P. phalangioides* (e.g. Uhl, 1993, 1994) as well as male pedipalp morphology and copulatory mechanism (Uhl *et al.*, 1995), interspecific interactions (e.g. Jackson & Brassington, 1987), sperm structure (e.g. Alberti & Weinmann, 1985), sperm storage secretions (Uhl, 1996), relation of web density to prey abundance (Roush & Radabaugh, 1993) and development of male pedipalp (Bartos, 1997). However, no quantitative analyses of male courtship have hitherto been carried out.

In this paper, the courtship and copulation of *P. phalangioides* are described, and some preliminary observations on the variability of male behaviour during courtship and copulation are presented.

### **Material and methods**

Young and adult individuals of *Pholcus phalangioides* (Fuesslin) were collected from a few town houses in Łódź and several cottages in Kampinoski National Park during the winter of 1995/96. The young spiders moulted to adulthood in the laboratory. The spiders were kept separately in glass containers (15 × 6 × 6 cm) covered with sponge stoppers. The rearing room was maintained at 18–25 °C. Twice weekly, the spiders were fed with four *Drosophila melanogaster*, and the rearing chambers moistened with about 1 ml of water. The spiders were allowed to mate in glass chambers (25 × 15 × 8 cm).

The process of courtship and copulation was observed in 39 males of *P. phalangioides*. Experienced or virgin males were introduced into chambers containing virgin females. The males were left in the chambers until the termination of copulation or, if copulation did not take place, for up to 5 hours. Copulation durations of 29 pairs were also measured.

The transition diagram method (Fig. 1), commonly used for description of interactions between individuals of a group (e.g. Jackson, 1978; Riechert *in* Witt & Rovner, 1982; Jackson & Hallas, 1986), was used to describe the spiders' behaviour during courtship. In Figure 1, the width of the arrow bars represents the approximate frequency of certain behavioural

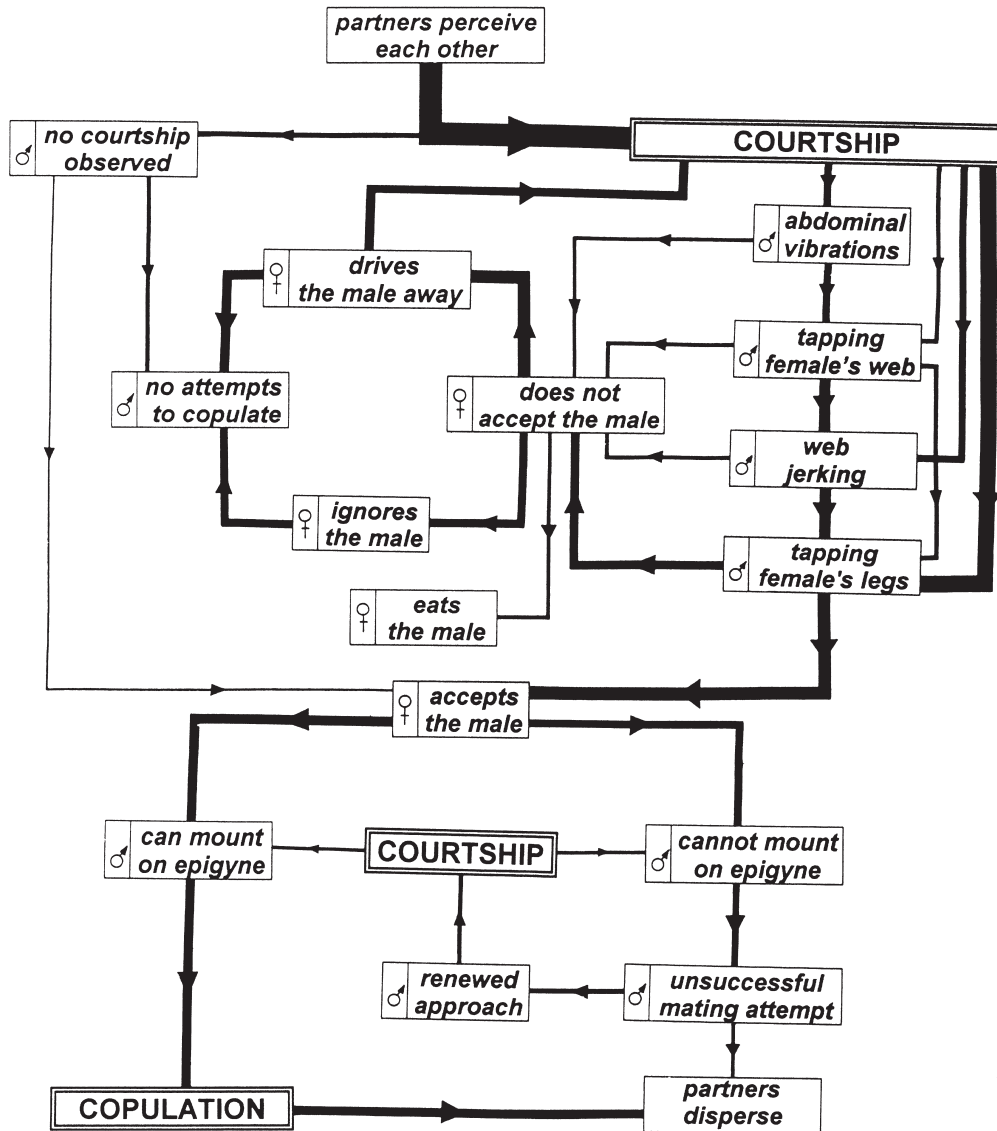


Fig. 1: The behaviour of male and female *Pholcus phalangioides* during courtship, mounting and copulation; width of the lines represents relative frequency of the behaviour.

elements e.g. the width of the top arrow bar leading from "partners perceive each other" equals 100% of the behaviour occurrence in the studied group of spiders. Frequency of other behaviours should be read as proportional to the width of the arrow bars leading to them in relation to the width of the starting arrow (100% of the behaviour occurrence).

## Results

In 32 trials (about 82% of studied spiders), males almost immediately initiated courtship (defined here, after Jackson (1978), as "heterosexual communicatory behaviour that forms the normal preliminaries to mating"). Six males (about 15% of studied spiders) did not show any interest in females and totally ignored them,

even when they were placed on a female. In one trial, no form of courtship prior to copulation was observed; however, the abdominal vibrations, which are difficult to notice, may have been overlooked.

Male courtship consists of four behavioural elements (Fig. 1): abdominal vibrations, tapping female's web, web jerking, and tapping female's legs. These elements, if all of them occurred, took place in a fixed order; however, the full behavioural pattern was noticed only in three trials. All these behaviours were accompanied by a slow approach of a male to a female. When a male could not directly approach a female because some lines of her web intervened, he cut them with his chelicerae. If a male could not insert his palp speedily and correctly into a female's epigyne, the female became reluctant and usually drove him away, or the male withdrew and, after a short time, tried again. In the latter case, the male again performed the three elements of courtship preceding the copulation (tapping female's web, web jerking, and tapping female's legs). The first behavioural element (abdominal vibrations) was never observed during renewed courtship. In this paper, "mounting" corresponds with both the initial coupling and the genital coupling described by Uhl *et al.* (1995).

**Abdominal vibrations.** Sets of very quick dorso-ventral vibrations with the abdomen, characterized by a low amplitude (Fig. 2a), performed about 4 cm from the female, only after the male has noticed her presence. The sets of vibrations took on average 68.5 seconds (shortest duration: 55 s; longest duration: 82 s;  $n = 2$ ;  $SD = 19.1$ ), and were the least common type of behaviour, observed only in three trials (about 8%;  $n = 39$ ).

**Tapping female's web.** A series of moderately violent strikes on the female's web to drumming on the female's web. The male tapped the web with a pair of legs simultaneously or alternately, mainly with legs I but sometimes also with legs II (Fig. 2b). The strikes were performed with the ventral surface of the tarsus, and with the legs slightly bent. This element of courtship behaviour lasted up to 20 minutes (with short breaks) (mean = 605 s; shortest duration: 240 s; longest duration: 1202 s;  $n = 8$ ;  $SD = 319.9$ ) and accompanied a slow approach by the male towards the female. When the male tapped the

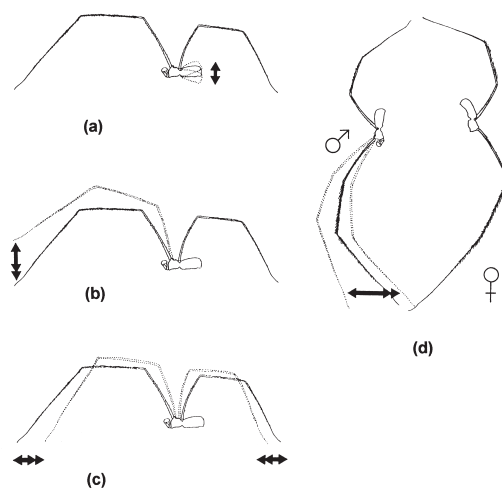


Fig. 2: Male behaviour during courtship. **a** abdominal vibrations; **b** tapping female's web; **c** web jerking; **d** tapping female's legs. Arrows show the directions and dynamics of the movement; double arrowheads represents more violent movement.

female's web he was about two body lengths away from her (about 2.5 cm). This element was observed in nine trials (about 23%;  $n = 39$ ).

**Web jerking.** A series of quick retracting and relaxing movements with all the legs. Tarsal claws were hooked on the web, resulting in an alternate increase and decrease of web tension (Fig. 2c). This element of the courtship usually lasted for a few minutes; each jerk took less than 0.5 seconds. The sequences of jerks, lasting on average 118 seconds (shortest duration: 50 s; longest duration: 205 s;  $n = 5$ ;  $SD = 59.0$ ), were separated by short periods of stillness and were accompanied by a slow approach of the male to the female. The male jerked the female's web close to her (but not near enough to touch her with his legs), or sometimes, just before coupling, if the female changed her position on the web or did not assume the acceptance posture (described below). This type of behaviour occurred in eleven courtship episodes (about 28%;  $n = 39$ ).

**Tapping female's legs.** Moderately strong striking of female's legs I and II, performed by the male with legs I drumming on the female's legs (Fig. 2d). The male tapped the female's legs whilst hanging on her web with his

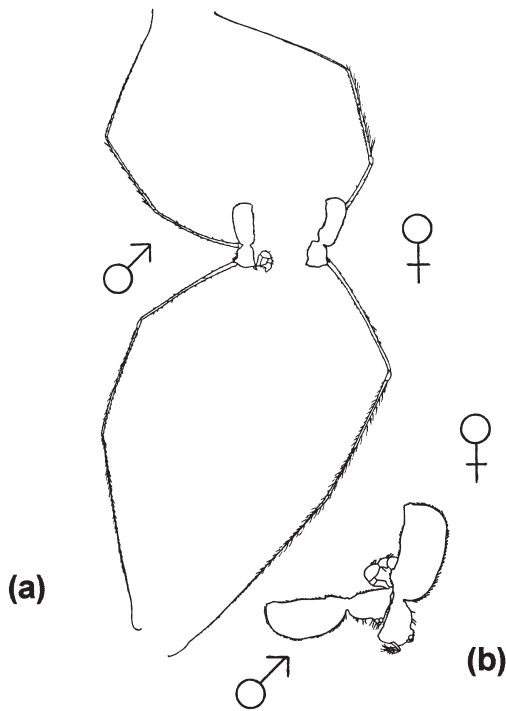


Fig. 3: Postures assumed by male and female *Pholcus phalangioides*. **a** before copulation; **b** during copulation.

cephalothorax downwards. This phase lasted from 100 to 1200 seconds (mean duration: 457.8 s;  $n = 9$ ; SD = 348.3), until the female either accepted the male or drove him away. The male tapped with breaks of different duration (every episode consisted of a few or several dozen single strikes). This element of behaviour was observed in 23 courtship episodes (about 59%;  $n = 39$ ) and directly preceded copulation.

During most of the male courtship, females remained motionless; however, from time to time they performed several slow, swinging movements with the body in a ventro-dorsal axis. The apparent sign that the female had accepted the male was her taking up a specific posture: all her legs were extended sideways and were kept motionless in this position until the genital coupling (Uhl *et al.*, 1995) began. However, lowering of the female's body reported by Uhl (1994) and Uhl *et al.* (1995) was not observed. In 26 trials (about 67%;  $n = 39$ ), the females responded aggressively to the

male courtship; however, they allowed copulation in successive males' trials. In two trials the males were eaten; this has not been reported before (Elgar, 1995). In both trials in which males were eaten, their behaviour appeared to be less vigorous in comparison to the behaviour of other courting males (their motions were slower, and one of the spiders fell off the female's web during courtship). Both males lacked leg I, lost during previous courtship events with other aggressive females. However, it cannot be excluded that cannibalism in rearing boxes may partly result from the confined space available for spiders, as suggested by Uhl (pers. comm.). A small number of the females did not respond to male signals at all, remaining motionless even when the males tapped their legs for about one hour.

Five out of 12 males accepted by the female could not locate an epigyne (they tried to copulate with the female's legs), or did not complete the initial coupling (Uhl *et al.*, 1995) at a single trial. Some of them were successful after several approaches, but others were driven away by the female. At the beginning of copulation, both spiders stretched their legs sideways in the same plane and trembled for a few seconds. After this they stopped moving, but a specific copulatory posture was maintained until the end of the copulation (Fig. 3). The males accepted by the females inserted the distal parts of their pedipalps and initiated the copulation (the copulatory mechanism was precisely described by Uhl *et al.* (1995), and will not be considered here). Mean copulation time was 71.7 minutes ( $n = 29$ ; SD = 44.3); the shortest, 8 minutes; the longest, 152 minutes (Fig. 4). Copulation was presumably terminated by the female, by performing jerky movements and manipulating the tarsi of legs I in the coupling area. After copulation, females always responded aggressively towards the males and drove them away.

## Discussion

The signals in the courtship of a male *P. phalangioides* are mostly web-mediated and based on non-visual cues, which is quite typical (in terms of signal types produced) for many web-building spiders (Witt & Rovner, 1982). They are also very similar to those in the related species *P. opilionoides* (Bartos, unpubl.). During

male courtship, three types of signals were generated: web vibrations, changes of web tension, and tactile signals. Web vibrations were produced when a male was vibrating with his abdomen, tapping the female's web and jerking on the web. Changes of web tension were produced during stretching and relaxing movements of a male jerking on the web. Tactile signals were generated during tapping of the female's legs. Vibrations with the abdomen had much higher frequency than other signals and they produced continuous web vibrations. During copulation, and at least the last phase of courtship, partners could use only vibratory and tactile signals to communicate and orient themselves, because during these phases their ventral sides were facing (Fig. 3).

As in most other spiders, one of the main functions of courtship is to suppress the female's prey-catching instincts (Witt & Rovner, 1982). This may be supported here by several observations of very aggressive responses of females to those males whose courtship behaviour was different from the one of accepted males (two cases of males lacking one of their legs I). These males appeared to be less vigorous in comparison to other males. The females reacted in the same way as when prey (fruit flies) was introduced into their containers. However, in response to the courting of a successful male, the female, after turning towards the male, became motionless and adopted the acceptance posture (*sensu* Robinson & Robinson, 1978); the interpretation of this may be that signals emitted by the male corresponded with the mate choice criteria of the female. The differences between the sets of signals produced by each male offered females an opportunity to choose between them. They may distinguish between males with different abilities to complete the insertion process quickly (they always refused to copulate with males which did not manage to mount after two or three trials). This observation, however, is different from Uhl's findings (pers. comm.). In the group of *P. phalangioides* she studied, as many as 100 trials could precede successful copulations. Male ability to complete palp insertion successfully is possibly correlated with the individual variation in functioning of their sensory organs and nervous system.

The mean duration of copulation in this study is very similar to one presented by Uhl *et al.*

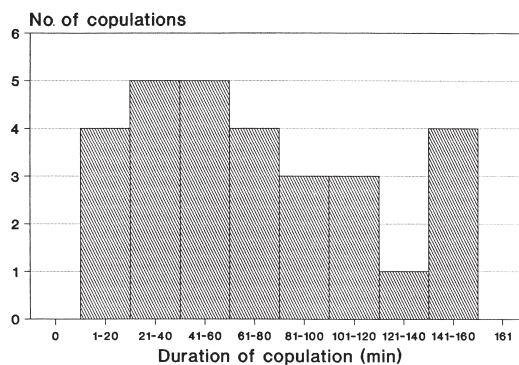


Fig. 4: The distribution of copulation duration in the studied population.

(1995) (mean copulation time, 64.5 min; shortest, 16 min; longest, 122 min;  $n = 42$ ;  $SD = 26.6$ ) and Reagan & Reagan (1989, *in* Uhl, 1993) (mean copulation time, 72.3 min; shortest, 10 min; longest, 304 min;  $n = 104$ ;  $SD = 43.3$ ). However, there is great variability between individual duration of copulations (weighted average  $SD = 39.5$ ) in these studies and those reported here. This result cannot be ascribed to individual female's status (all were virgin). It is also unlikely to be connected with male status (virgin and experienced males were used), since copulation duration experiments with inexperienced and experienced males carried out by Uhl (1993), and Yoward (1996) gave results not statistically different (Uhl, 1993, and pers. comm.). However, it may be connected with other male individual characteristics, such as courtship vigour, precision, and time needed for insertion. More observations are needed to investigate the cues which females use during courtship and copulation to explain why some males copulate for 304 minutes (Reagan & Reagan, 1989, *in* Uhl, 1993) and others for only 8 minutes (this study).

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