

Observations on the sexual behaviour of *Porrhomma egeria* Simon (Araneae: Linyphiidae)

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Introduction

Porrhomma egeria Simon is a predominantly cavernicolous species with an extensive European distribution (Locket & Millidge, 1953; Simon, 1884; Thaler, 1968; Tretzel, 1956; Miller & Kratochvil, 1940; Bourne, 1977b). As with other cave-dwelling species of the same genus (*P. myops* Simon, *P. convexum* (Westr.), *P. rosenhaueri* (L. Koch) and *P. subterraneum* Simon) very little is known concerning its biology and ecology (Bourne, 1977a, 1977b). This is due perhaps to the rarity of these species and the difficulties encountered in collecting and breeding cavernicolous spiders.

Among the few papers devoted to the sexual behaviour of Linyphiidae, that of van Helsdingen (1965) gives the most interesting account. The observations made by Locket (1926) although incomplete give useful information on the courtship behaviour of three species of *Linyphia* and of *Lepthyphantes*.

Material and methods

Adult *Porrhomma egeria* were collected on 30 January 1977 in the Bange Cave (Haute-Savoie, France) where an important population was known to exist (Bourne, 1977b). At this time it is possible to collect the maximum number of male specimens. The spiders were placed individually in small bottles containing a small quantity of damp clay. Past experience with cavernicolous spiders has revealed their sensitivity to sudden changes of humidity and the usefulness of damp clay in overcoming this problem.

The spiders were transferred to a cellar and placed in small breeding jars (diameter 6 cm, height 4 cm) containing sterilized pebbles and clay. The substrate was kept constantly moist by the addition of a few drops of water every week and the temperature was

checked daily. The temperature oscillated between 6 and 8°C during the month of February. Every three days, all the spiders were fed with male *Drosophila melanogaster* Meig. (vestigial wing).

General behaviour under laboratory conditions

After three days of captivity all the females had spun irregular webs among the pebbles and were hanging on the underside of these webs. None of the males had spun a web, only a small dispersed collection of threads on the underside of the glass jar lid.

Following the placing of a fly on a female web, her first reaction was to move away from it. If the fly was struggling to free itself the female quickly approached the fly, tapping the web with her forelegs. As soon as contact was made with the fly the female climbed onto it, stabbing it with her chelicerae. The prey was not wrapped in silk in this species, or in two other species studied in the genus (*Porrhomma myops* Simon and *P. convexum* (Westring)).

When not feeding, the spiders remained motionless on the underside of their web or on a pebble and every now and then could be seen "preening" their legs (passing one leg after another between their chelicerae).

Sexual behaviour

The following analysis of the sexual behaviour of *P. egeria* was made after observing three successful, one unsuccessful and several incomplete copulations between 9 and 19 February 1977. Up to now I have not been able to observe a complete successful copulation (courtship + copulation) for either *P. myops* or *P. convexum*. However some similarities of behaviour between these two species and *P. egeria* will be discussed.

The conditions under which the spiders were observed were as follows:— temperature: 15-18°C; relative humidity: 90-100%; Lux: less than 600. All the observations were made under a binocular stereoscopic microscope (magnification x12) using a cold light source.

For practical purposes courtship and copulation have been divided into seven consecutive phases (Fig. 1).

Phase 1. Introduction of male onto female web

After an initial moment of "panic" caused by manipulation, the male begins walking aimlessly around on the upper surface of the female web. He stops now and then to "preen" legs and palps. He then moves to the underside of the web, usually by passing around the edge of the web. Sometimes he will climb down off the web on to the substrate and then regain the web on the underside. Finally contact is made with the female on the underside of the web. During this introductory phase the female remains motionless.

Phase 2. Male/female contact

As soon as the male touches the female she moves away briskly and the male stops all movement. The female quickly "charges" the male who runs off to the far side of the web or may even leave the web. "Charging" consists of the female rushing towards the male and when contact is made she stops; she does not follow the male. This phase may be repeated several times but eventually the only reaction of the female to contact with the male is that she moves away.

Phase 3. Beginning of courtship

The male moves around on the underside of the web making small "jerking" movements, stopping now and then to preen his palps. The jerking movement, which dominates the male courtship behaviour, consists of slowly lowering the cephalothorax followed by a rapid movement upwards. When repeated several times this movement has certain resemblances

to "press-ups". It appears that a certain mechanical resistance at the base of the legs (coxae) is responsible for the jerky nature of this movement, and this may involve the stridulatory organs of coxae I (Locket & Millidge, 1957).

During these movements he simultaneously reinforces the web with small lengths of thread. The female remains motionless. The intensity of the jerking increases and becomes associated with palp drumming on the web. "Drumming" is a simple alternate tapping of the web with the palps and is not a rapid movement. Once the male has relocated the female he approaches her, tapping delicately with his forelegs. She generally reacts by taking up a crab-like position and by retreating away from the male. The time taken to complete this phase for the three successful matings was as follows: 12, 21 and 40 minutes.

Phase 4

The male moves on the web turning around either in a small circle or in a short spiral. This is a rather complicated behavioural movement and is also found in two other species of this genus (*P. myops* and *P. convexum*). It can be best described by the following summary:

- (i) backward movement away from the female
- (ii) male turns around in a complete circle on the underside of the web or occasionally in a small spiral (circle + half a circle)
- (iii) male completes the movement orientated in the same direction as at the beginning of the exercise. He may be closer or further away from the female.

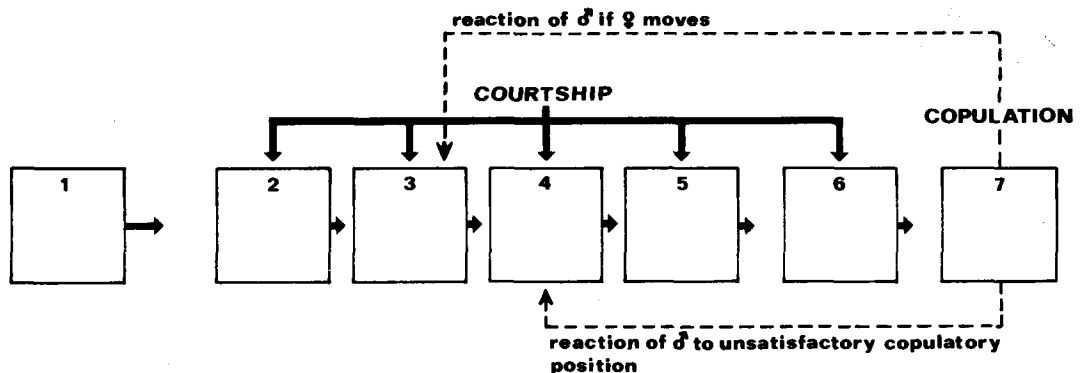


Fig. 1: Principal phases of the sexual behaviour of *Porrhomma egeria* (1-7 = phases: see text).

It must be noted that on most occasions the male is web building during this phase. In the meantime the female may either remain motionless or pluck the web with her forelegs. This phase is usually fairly short (minimum 6 mins) but can exceed 20 minutes.

Phase 5

The male approaches the female tapping violently with his forelegs while jerking "frantically". Leg tapping is invariably carried out by the forelegs extended in front of the male. At first (in phase 3) the movements are rather timid but towards the end of the courtship phases the rhythm is such that the legs appear to be vibrating. The tactile nature of leg tapping is apparent and it is possible that the rhythm informs the female as to the readiness of the male to copulate. It is at this stage of courtship that the female turns to face the male and if he is tapping her on the abdomen she may have to turn through 180° in order to face him. This is a short phase and lasts no longer than 5 minutes.

Phase 6

When the male and female are facing each other the female will reply to the male's tapping by tapping

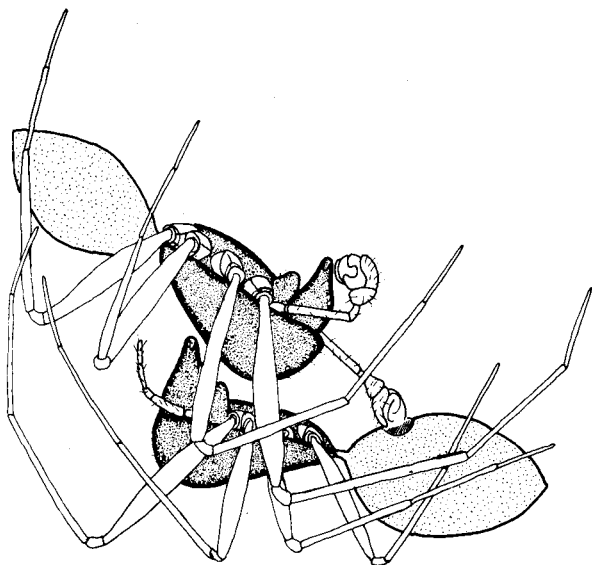


Fig. 2: Schema showing typical copulatory position of spiders of the genus *Porrhomma*. (Legs shown only on one side; details of palp-epigyne contact not given).

his forelegs with her forelegs. This appears to be a signal for the male to move into the copulatory position.

Phase 7. Copulation

The male moves into the copulatory position (Fig. 2). If the distance between the two spiders is satisfactory the outstretched male palp can be hooked onto the epigyne without any difficulty. From this moment the male undertakes the following sequence of movements:— the left palp is hooked onto the epigyne and then returned to his mouth where "nibbling" occurs; in the meantime the right palp is hooked onto the epigyne. He then brings the right palp to his mouth for nibbling while the left palp is rehooked onto the epigyne. During the palp-epigyne contact the haematodocha swells up to about twice the volume of the entire palp when at rest.

"Nibbling" consists of biting the embolic division (not clearly visible under the conditions of observation) between the chelicerae. It appears that a whitish liquid is accumulated in the mouth region during this activity and that during the interruptions in copulation the male places small droplets of this liquid on the web. Van Helsdingen (1965) observed a similar phenomenon during his study of *Lepthyphantes leprosus*. The nature and function of this liquid is unknown.

Once copulation has begun the female normally remains motionless while the male performs the palp-to-epigyne-to-mouth movements. At first these movements are rapid (as many as 20/minute) but after an hour or so they become much slower while the epigyne-palp contact becomes longer (Fig. 3).

From the observations made it appears that copulation may be interrupted for two principal reasons and that the behaviour of the male following an interruption is different in the two cases. Firstly, if the female moves the male will briskly retreat from her. He then takes up the courtship behaviour from phase 3 (Fig. 1). Secondly, if for one reason or another the male is no longer in a satisfactory copulatory position and has difficulty in hooking his palps onto the female epigyne he backs away from the female. In this case, however, he will take up the courtship behaviour by making a circular movement (phase 4) and quickly re-enters the copulatory phase.

Copulation lasts at the most for 14 hours, and

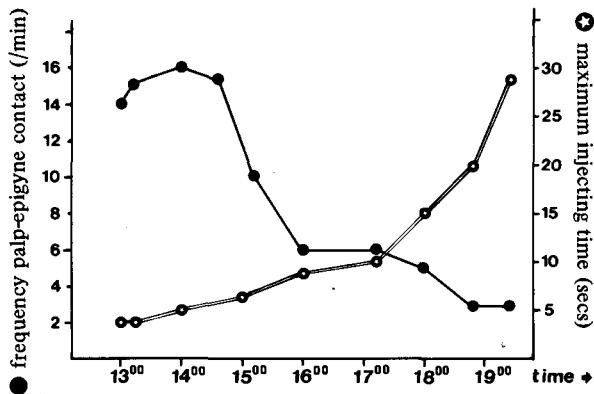


Fig. 3: Frequency of palp-epigyne contact during first 6 hours of copulation for *Porrhomma egeria* (2nd successful copulation), and maximum duration of injection periods.

only the second pair of spiders were observed during the whole operation which lasted 8.5 hours. It appears that at the end of copulation, following a rapid movement of the female, the male tries to take up courtship from phase 2, but the aggressive reaction of the female is such that he is "forced" to take refuge on the upper side of the web. The male remains sexually excited for several hours after a successful copulation and when on one occasion such a male was placed in the same jar as another male he began reacting as if he was confronted with a female.

Proof of successful copulations was given by the hatching of young spiders from the cocoons built by the females. The development of several species of *Porrhomma* will be described in a later paper.

Conclusions

From the above observations and results not yet published of unsuccessful copulations of *P. myops* and *P. convexum* it appears that the courtship and copulation is of a simple kind. The aggressivity of the females is greatly reduced and only consists of perfunctory attacks on the male in the introductory phase (2) of courtship and at the end of copulation. The comparative passivity could be an advantage for species living mostly in caves where encounters between males and females would be more precarious than in epigeal habitats. The success of certain populations of cavernicolous *Porrhomma* would suggest, however, that the cave habitat has little limiting

effect and that the lack of competitive carnivores has allowed the establishment of important populations (Bourne, 1977a, 1977b). Platnick (1971) citing Mayr points out the importance of change of behaviour brought about by a shift to a new niche (eg. epigeal to hypogean habitats). The clear tendency of the species of this genus to occupy either cavernicolous or endogeous habitats may be one of the factors influencing the sexual behaviour.

The success of the three copulations analysed in this paper was confirmed by the egg-laying of the females and subsequent hatching of the young spiders. Thus it is clear that the males had sperm-filled palps prior to courtship. This is confirmed by the fact that one of the males had undertaken the maturity moult (6 February 1977) a few days before copulation and that he was not seen to fill his palps during either courtship or copulation. Unlike that of *Leptyphantes leprosus* as described by van Helsdingen (1965), copulation is of a simple type where palp filling is independent of copulation. This supports the statement of van Helsdingen (1965), that in the present state of our knowledge of the sexual behaviour of Linyphiidae it is not possible to make generalisations at the family level.

There remains the possibility that the females used were gravid, as Dr P. J. van Helsdingen pointed out (pers. comm.). From my observations it would appear that following a successful copulation females will not tolerate males on their web. However the period during which this aggressive behaviour is sustained after copulation is unknown.

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