

Courtship and mating in the social spider *Phryganoporus candidus* (Araneae: Desidae)

Michael F. Downes

Zoology Department,
James Cook University,
Townsville,
Queensland 4811,
Australia*

Summary

The cribellate spider *Phryganoporus candidus* (= *Badumna candida*) (L. Koch) was found to adopt a mating posture known in cribellate spiders but apparently unrecorded among cribellates. Courtship lasted for a mean time of 92 min and involved mutual interplay of the partners' forelegs, a behaviour common in non-sexual encounters at all stages of the life history of *P. candidus*. The mean duration of 23 observed copulations was 245.4 min and involved up to several hundred palp-epigyne engagements. Both males and females were capable of multiple matings, but females rarely produced egg sacs in captivity.

Introduction

Spiders exhibit complex and variable courtship behaviour. Whether the suppression of predatory instincts (Platnick, 1971), species recognition and discrimination (Paterson, 1985), sexual selection (Eberhard, 1985), or all of these, are major driving forces in the evolution of this complexity remains unresolved. Opinions differ also on the significance and relative extent (compared with non-sexual behaviour) of the variability that attends the courtship patterns of spiders (Robinson & Robinson, 1980; Robinson, 1982) and other arthropods (e.g. Ritchie, 1992). Wide variations in courtship repertoire are known (e.g. Jackson & Whitehouse, 1989), but there is also evidence that favours Paterson's (1985) view that courtship behaviour is still relatively conservative (e.g. Lambert & Harper, 1985; Baptista & Trail, 1988).

If it is acknowledged that mating behaviour is closer even than courtship behaviour to the cutting edge of reproductive success, mating might be expected to show even less variability than pre-mating signals and activity. Nonetheless, many variants of copulatory posture may be found within some families of spiders (Robinson & Robinson, 1980; Robinson, 1982). The variations that occur make suspect any taxonomic implications of copulatory posture, but among the generalisations that seem to remain valid to date is that the cribellate families, considered by most arachnologists to be monophyletic, exhibit the "primitive" mating posture in which the participants engage face-to-face, thence venter-to-venter (Foelix, 1982).

The cribellate desid *Badumna candida* (L. Koch), widely distributed on the Australian mainland, is one of three species that together form the *candida* species group of the genus *Badumna* (Gray, 1983; Colgan & Gray, 1992). A current revision, unpublished at the time of writing, proposes that *Badumna candida* revert to

Phryganoporus candidus (L. Koch) (M. R. Gray, pers. comm.). Consequently, the latter name is used here. *P. candidus* is a periodic-social spider, i.e. one in which juveniles coexist in the same nest but disperse before they mature and hence outbreed (Kullmann, 1972). Its sheltered retreats are constructed of silk-bound leaves (Main, 1971), and courtship and mating occur within these retreats in February and March (Downes, 1993). The present study was confined to laboratory observations.

Materials and methods

The 112 spiders used in this study were collected as middle or late-instar juveniles, from numerous different nests in a 400 ha study site surrounding James Cook University, Townsville. They matured in isolation in the laboratory and were thus all virgins at the time of their first encounter. Mature males were evident by their fully-developed palpal intromittent organs (Gray, 1983; 251, figs 1–3). Female maturity was confirmed by the presence of the conspicuous sclerotised crossbar of the epigyne (Gray, 1983: 251, fig. 4), not found in subadult females.

Arenas were glass containers (50 mm tall × 25 mm diameter) with perforated plastic stoppers. Previous experience showed that these dimensions were more than adequate, since in larger containers courtship always took place in a small, restricted area. Mature females were allowed to inhabit these containers for ten days before a trial, to establish a web. Females and males were well fed during this time. The photoperiod was about 13 h light, 11 h dark, and temperature ranged from 22–26°C. For each of the 48 trials, a mature male was placed in a female's container, after randomising the selection of the pair. No spider was used more than once in this part of the study.

Each trial lasted six hours, a trial length based on previous informal observations of courtship and mating. Trials commenced in the late afternoon, a time when the spiders normally became active in field nests (Downes, 1994). Room lighting was reduced to the minimum necessary for observation. Observations were continuous during each trial, and times (from the start) were recorded for first foreleg interplay, first mating engagement and final separation. Sometimes two or more (up to five) trials were conducted simultaneously. Observations were not made on haematodochal pulsations, nor were female genitalia examined subsequently for the presence of plugs.

Thirteen of the spiders involved (seven females, six males) were later the subjects of remating trials, conducted under the same conditions as described above. All remating partners were spiders other than those used in the 48 courtship/mating trials. Similarly, three of the six males used in remating trials were subjected to third-mating trials.

Results

Courtship

Courtship between mature males and females varied widely in duration and in the frequency and intensity of

*Present address: Department of Zoology, Universitetsparken B 135, DK 8000 Aarhus C, Denmark.

the behavioural components, but always included palp-drumming by the male and the mutual interplay of the forelegs (primarily legs I) of both partners. In addition, courtship often (i.e. with a frequency >50%) included cheliceral nipping gestures directed by the male at the female's face, and brief retreats by the male to rub his palps with his forelegs. Sperm induction (charging of the palps with sperm) was not observed.

Of the 48 trials conducted, 23 led to mating; of the other 25, 21 developed into a stationary stand-off after one or more attempts by the male to establish leg contact, and four resulted in the male being chased by the female until he was removed and the trial terminated. The stationary stand-offs were terminated without further incident at the end of the trial period (six hours). Of the 23 trials that did lead to mating, the shortest period between the start of the trial and the first mating was 30 min, the longest 210 min (mean = 92.0, SD 44.1 min). The number of bouts of foreleg interplay, and the duration of these bouts, was not always recorded; in one case there were three such bouts, in others 20 or 30. It was sometimes unclear whether a pause between bouts had occurred, or whether a separation of partners between bouts was complete. The shortest time from the start of a trial to the first foreleg interplay was three minutes. This particular courtship led to a stand-off. For a courtship that led to mating, the shortest time to first foreleg interplay was six minutes.

Mating

The aspects of mating behaviour observed and described here were less variable than those of the courtship behaviour, the main source of difference between the 23 matings being the overall duration. One atypical mating lasted only 25 min, after which further attempts by the male to engage his palps were rebuffed by the female and a stand-off ensued. The remainder varied from 128 to 355 min (mean = 245.4, SD 51.8 min), excluding one instance in which the observations had to be terminated while the pair were still *in copula*.

The mating position (Fig. 1) was that of fig. 2b, p. 311 of Bristowe (1929). The spiders faced in opposite directions, the male standing over the female with his venter to her dorsum. The male reached to his right and left alternately, extending his left palp under the female when he reached to his right (i.e. to the female's left) and extending his right palp under the female when he reached to his left (i.e. to the female's right). When *in copula* in each case, the male had to stand a little clear of the female and lean down far enough so that he was standing more beside than over her. His anterior-posterior body axis was pitched forward at up to 45° relative to that of the female, and he held this position *in copula* for up to one minute. It was the dorsal surface of the palp that was applied to the female epigyne. To transfer from one side to the other he had to move through about 140° across the top of the female and down her other side. The female remained immobile during the mating, doing nothing to facilitate intromission.

Given the usual duration (less than one min) of a single mating engagement, and the fact that the transfer of the male from one side to the other of the female was rapid by comparison, normally taking less than 10 s, up to several hundred separate palp/epigyne engagements were undertaken during mating in *P. candidus*.

Females were sometimes sufficiently aggressive towards males after mating to necessitate separation before the six hours of the trial was completed. Males were cannibalised after mating on three occasions.

Multiple matings

Among females, there were three dual matings, one being separated by seven days, the other two by 14 days. No behavioural differences were detected between first and second copulations. The duration of the second matings, for example, did not differ from those of the first matings of the same spiders ($t = 0.66$, $p > 0.50$, or from the mean value for all recorded first matings by females ($t = 0.83$, $p > 0.20$). Four other attempts at remating single-mated females were unsuccessful, resulting in a stand-off or aggression.

Among males, six instances of dual mating were recorded (each pair of matings separated by periods ranging from five to 42 days), and three instances of triple mating (separations being 12 and 30 days, 14 and 19 days, and 30 and five days). No attempts at remating single-mated (or dual-mated) males were unsuccessful.

The durations between matings were of course at the choice of the experimenter; however, the lowest values in each case show the potential minimum periods between matings.

Egg production

Only three of the mated females subsequently produced egg sacs. One produced an ill-constructed sac containing but a single egg (which did develop

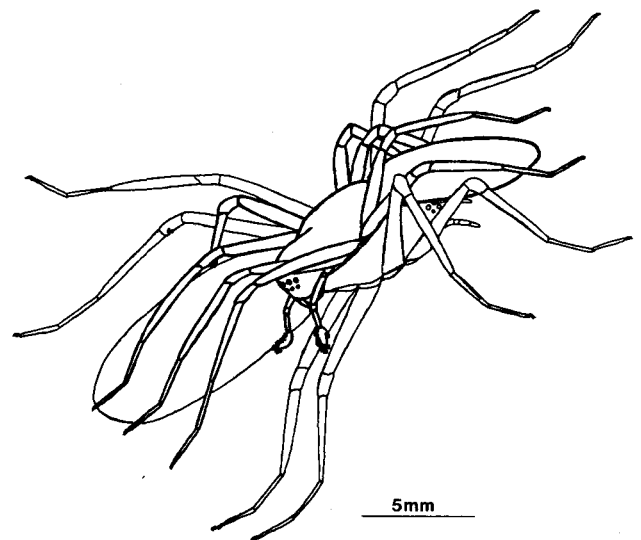


Fig. 1: The mating position of *P. candidus*. The partners face in opposite directions. The male overlies the female and extends his palps alternately on each side, to reach her ventrally-placed epigyne.

normally). Another produced two properly-made sacs, one of which contained 12 and the other 20 inviable eggs. The third, a dual-mated female, constructed an ill-made sac which produced four spiderlings.

Discussion

Courtship

Sperm induction in *P. candidus* evidently occurs before courtship, as in *Dictyna volucripes* Keyserling (Starr, 1988) and many other spiders (Robinson, 1982). Interplay of forelegs was not only a universal feature of courtship behaviour among *P. candidus* adults; it was also the only conspicuous interactive behaviour I observed among juveniles of all ages in natural nests in the field (Downes, 1992). Jackson (1979) notes the same behaviour for *Mallos gregalis* (Simon), but in *D. volucripes* the second, and occasionally the third, pair of legs is used by males to stroke females during courtship (Starr, 1988). The variation in the occurrence and frequency of cheliceral nipping and palp-rubbing is in accord with variation in the sexual behaviour of other spiders (e.g. Starr, 1988; Jackson & Whitehouse, 1989).

The duration of courtship (leading to mating) in *P. candidus* varied widely, but even the shortest recorded time exceeded the maximum (13 min) given for *Mallos trivittatus* (Banks); on the other hand, the maximum recorded for *P. candidus* was shorter than the minimum (231 min) given for *Dictyna calcarata* Banks (Jackson, 1979).

Mating

The mating position was Bristowe's (1929) Class B, which is not recorded by Bristowe for cribellate families. Later workers, for example Von Hilversen (in Foelix, 1982), essentially confirm and extend Bristowe's summary, listing four classes of mating position. Although many variations of copulatory posture may occur within a single family (Robinson, 1982), the spiders that characteristically adopt the copulatory position in which the male goes over the top of the female, his venter to her dorsum, are the "modern" wandering spiders such as salticids and lycosids. This mating orientation apparently evolved more than once among ecribellates (Bristowe, 1929), but along with *Badumna longinqua* (L. Koch), which adopts the same mating posture as *P. candidus* (M. R. Gray, pers. comm.), the present findings may be the first record of a cribellate spider adopting this posture during mating. Males of *Stegodyphus sarsinorum* Karsch take up a position ventral to the female (Jacson & Joseph, 1973; Bradoo, 1975), as do males of *Dictyna volucripes* (Starr, 1988); and Jackson (1979) lists seven other dictynids that do the same. Jackson also lists *Ixeuticus longinquus* (*Badumna longinqua*) as behaving like these other dictynids, but this record is based on Gregg (1961); Gregg's spider was not *I. longinquus* but *Corasoides australis* Butler (M. R. Gray, pers. comm.). However, Forster & Wilton (1973) include *Corasoides* in the family Stiphidiidae, and moot the possibility that

this genus may have become secondarily ecribellate; if so, it may not be out of context in the present discussion after all.

Several hundred mating engagements is probably not an unusually high number for spiders. It is comparable, for example, with the mean total number (316) of palpal insertions made during copulation by the lycosid *Schizocosa avida* (Walckenaer) (Rovner, 1973). Likewise, post-mating, and even pre-mating, aggression and cannibalism of the male is not remarkable among spiders (Buskirk *et al.*, 1984; Newman & Elgar, 1991).

Multiple matings

Since 23 of 48 courtship trials (48%) involving unmated females led to mating, and three of seven trials (43%) involving previously mated females did so, there was no evidence to suggest that female receptivity differed between virgin and mated females.

Different males were involved in the matings that gave rise to egg sac production, so the study did not demonstrate that males can successfully inseminate more than one female. However, the multiple matings recorded for males, and the number of palp-epigyne engagements in a typical mating, suggest that they can do so.

Multiple-mating capabilities of males are necessary for local mate competition and female-biased sex ratios among social spiders (Aviles & Maddison, 1991). These traits, however, are not evident in this population of *P. candidus*, because females disperse before reaching maturity (Downes, 1993). Electrophoretic evidence on genotypes in colonies of *P. candidus* in the Perth district of Western Australia (Ayre, 1977) suggests that the multiple-mating capabilities of female *P. candidus* are rarely realised in natural populations.

Egg production

In contrast with the numbers and fertility of eggs in laboratory-made sacs, the mean number of eggs in sacs in naturally-occurring nests is 26.9, SD 6.57 ($n = 130$), and fertility is high (Downes, 1993).

The general failure to oviposit in captivity was consistent with the behaviour of numerous field-collected mature females of this species at all stages of their iteroparous egg-laying cycle, when kept in artificial conditions in the laboratory, and does not therefore imply that the observed matings mostly did not result in inseminations. Four egg sacs, two of which produced viable young, from 23 females, was a better oviposition record than the 12 egg sacs (five viable) produced by hundreds of fertilised females maintained in the laboratory over several years (Downes, 1992). Unless parthenogenesis was occurring, the production of live young in two instances in the present results demonstrates that in these cases at least, the matings were successful and oviposition of fertile eggs was not fully inhibited. The oviposition inhibition that evidently prevailed may have been an indirect effect of a prior nest-building inhibition: in natural conditions, subadult *P. candidus* females always construct a small funnel of

tough sheet-silk when founding a new nest after summer dispersal, and almost invariably attach their first egg sacs to that funnel; they never construct such funnels in captivity (Downes, 1992).

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Addendum

The research note by Fernando Costa (COSTA, F. G. 1993: Cohabitation and copulation in *Ixeuticus martius* (Araneae, Amaurobioidea). *J. Arachnol.* **21**: 258–260) came to my attention while this paper was in proof. Costa's observation, and not my own, is the first published record of a cribellate spider mating in the described fashion, if no previous records of the kind exist.