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Sperm Storage and Repeated Egg Production in Female *Pholcus phalangioides* Fuesslin (Araneae)

par
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Summary: 35 Female Daddy-long-legs spiders were allowed to copulate only once. Each individual female was kept separately for up to 375 days after copulation. Mating took place after an average of 8 days after the moult to adulthood. Egg-sac production of 35 females was recorded. Hatching success of the spiderlings was recorded for the egg batches of 32 females.
All except one female produced at least one egg-sac. Some produced up to 6 batches of eggs during the registration period. The hatching success of the spiderlings was high even after repeated egg-sac production.
Ph.phalangioides does not possess any concrete sperm storage organs such as receptacula. Sperm is stored in the genital cavity (uterus externus), embedded in glandular secretions discharged from two gland structures situated in the posterior part of the uterus externus. Nevertheless, the sperm mass does not get flushed out with one egg-laying process, which would call for repeated insemination. On the contrary, females of *Ph.phalangioides* are able to produce more than one fertilized batch of eggs, despite of their "primitive" bursal storage mode.

1. INTRODUCTION

Pholcus phalangioides is quite abundant in houses and cellars. Sheltered from extreme climate, reproduction is not restricted to the warmer seasons. Therefore, Daddy-long-legs spiders are easy to work with in respect of reproductive behaviour.
Female spiders store sperm in receptacula seminis for prolonged periods of time. Sperms are transmitted and stored in an encysted state i.e. encoiled and surrounded by

a secretory envelope (ALBERTI 1990). In *Ph.phalangioides*, like in other so-called haplogyne spiders, the sperm might get stored in the genital cavity (uterus externus or bursa copulatrix) (WIEHLE 1967, KOVOOR 1981). If this was true, the sperm mass would be easily flushed out with the passage of each batch of eggs and repeated mating would inevitably be necessary (FORSTER 1980). The reproductive behaviour of *Ph. phalangioides* was examined to find out how many egg-sacs a female is able to fertilize with the sperm of one single mating. The results help to estimate the actual constraints being imposed on such a haplogyne structure.

2. MATERIAL AND METHODS

Juvenile individuals of *Ph.phalangioides* were collected from the Zoological Department and from homes around Freiburg i.Br.. They were kept individually in plastic boxes of 10x10x7 cm (LxWxH). After the moult to adulthood the spiders were kept in couples in slightly bigger boxes (17x9x6,5 cm). During the day, male and female had access to each other. They were checked at least every 30 minutes. At night, the male was kept separately from the female partner, being enclosed in a plastic vessel within the plastic box. The couples were allowed to copulate only once. After copulation the females were kept separately in the smaller rearing boxes for up to 375 days.
Egg-sac production and the emergence of first-instar nymphs were recorded and the hatching success was determined as the number of spiderlings which emerged from an egg-sac in relation to the total number of eggs laid.
The rearing room was maintained at 23 to 28°C under constant photoperiod (14L-10D). The spiders were provided one fly (*Musca domestica* or *Lucilia spec.*) every 7 days.

3. RESULTS

From final moult to mating adult individuals took 8.3 days on average (n=35, sd=3,3) (figure 2). After one single copulation, 32 of 35 females produced more than one batch of eggs (91%) (figure 1). 54% made 3 or 4 egg-sacs. 4 spiders produced 6 egg batches. The results do not indicate the highest possible number of egg-sacs produced by one female. Rather, the data relate to the egg-sac production achieved during the registration period.
The time intervals from the production of one egg-sac to another varied greatly within a single individual and in comparison with other individuals (figure 2). Figure 2 shows that in a similar time period some individuals produced up to two egg batches more than others (e.g. no.24 compared with no.31).
The spiderlings hatch 16,7 days on average after egg laying (n=30, sd=2,8). The female enhances the hatching by eliminating the silken threads that hold the eggs together. The number of eggs in each egg-sac and the number of spiderlings that hatched from

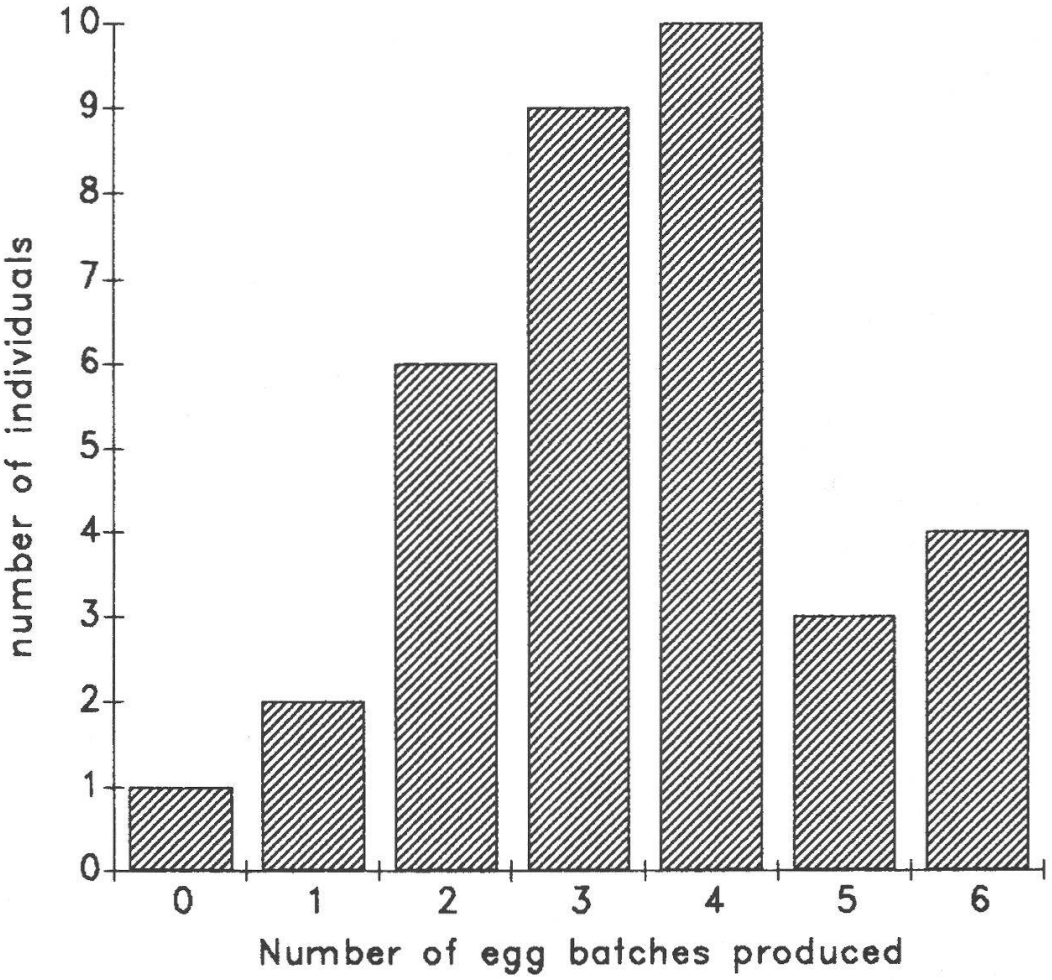

Fig. 1 - Egg-sac production by 35 females of *Pholcus phalangioides* during the registration period.

the egg-sacs are shown in figure 3. The hatching success differs greatly from egg batch to egg batch. Females which did not succeed in producing fertile eggs for example in the first egg batch, were mostly able to produce a high percentage of viable offspring in the following egg-sacs, some with up to 100% hatching success. Even after repeated egg-sac production the hatching success could be very high. Some females stored viable sperm up to one year.

In *Ph.phalangiodes*, sperm is stored in the genital cavity, in the so-called uterus externus. In order to hold the sperm in a fixed position, a glandular secretion is discharged from two complex gland structures situated in the posterior part of the uterus externus (these results will be published elsewhere in detail). The entire filling of the genital cavity coincides with the onset of the mating behaviour. Semithin sections of the genital cavity show that the secretory product is built up in the course of about 8 days after the final moult.

Females are able to fertilize more than one batch of eggs although after oviposition only a few clumps of sperm are left in the genital cavity, mostly close to the heavily sclerotized valve or the glandular pores. The remaining sperms are encoiled and nonflagellate.

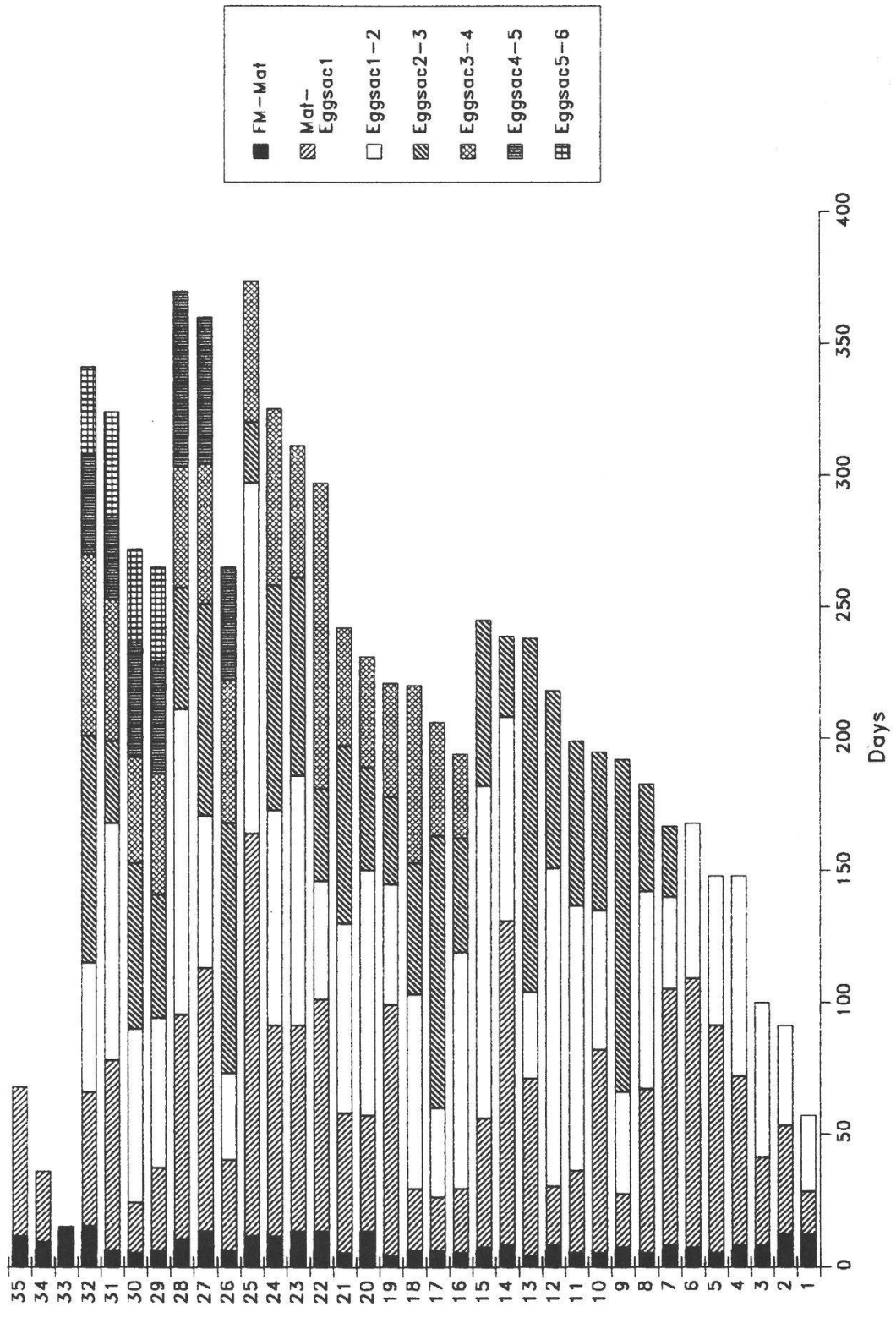

Fig. 2 - Periods of time elapsed between the final moult and mating (FM-Mat) and between one egg laying and the following egg laying of *Pholcus phalangioides*. The individual reproductive history is given for 35 females, whose numbers correspond with those given in fig.3.

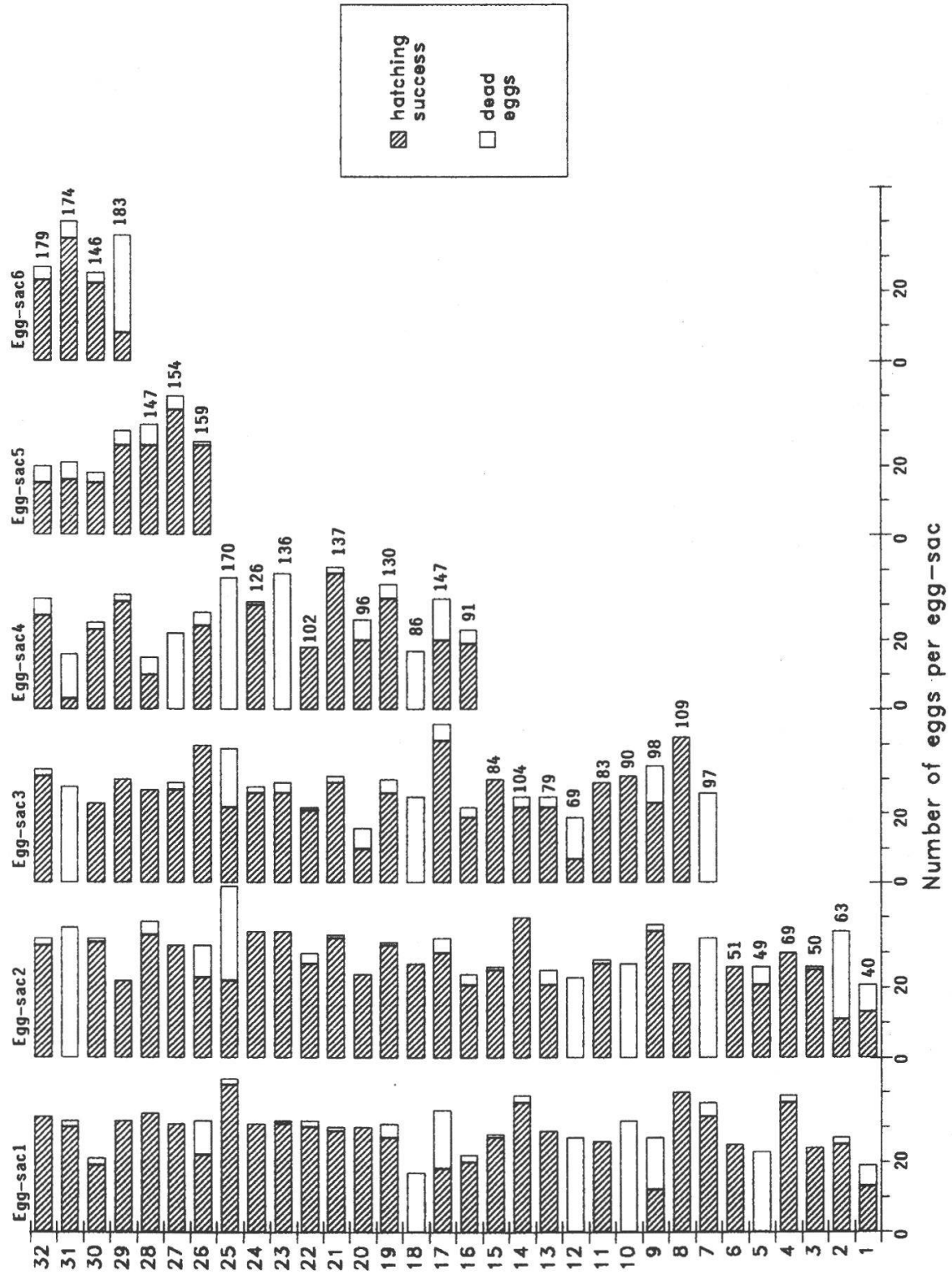

Fig. 3 - The reproductive success of 32 females of *Pholcus phalangioides*. The amount of eggs laid per batch and the number of spiderlings that hatched from each batch of eggs are given. The figures at the end of the bars represent the total number of eggs laid by the individual female during the registration period.

4. DISCUSSION

Female Daddy-long-legs spiders copulate about eight days after their final moult. Apparently, this is the time required for the glandular cells of the uterus externus to mature and to fill the genital cavity with glandular secretions. If the female would not provide a matrix for the sperm to be stored in, the sperm could possibly get lost through the genital opening. Therefore, I consider the prime function of the secretion in fixing the sperm mass in a specific position. This phenomenon is also known from various Coleoptera. Females of *Speonomis delarouzeei* (Catopidae) mate only 24-32 days after the moult to adulthood, as the spermathecal accessory glands take this long to develop and to discharge their products into the pouch of the spermatheca (JUBERTHIE-JUPEAU & CAZALS 1985). Also, in mealworm beetles (*Tenebrio molitor*) a high percentage of females copulate only after the spermatheca is fully filled with secretory products, which takes four days to accomplish (HAPP & HAPP 1970). Another beetle, *Aleochara curtula* (Staphylinidae), is known to possess spermatheca filled with secretions when willing to mate (GACK, pers.comm.). The coincidence of receptivity and filled spermatheca probably is a general phenomenon in arthropods that has not yet been payed attention to.

The time intervals from one egg-laying to another were irregular, which is possibly due to the rearing conditions (temperature differed greatly). However, the results of MIYASHITA (1988) show that despite of constant rearing conditions cocoon production was irregular. He stated a tendency of increasingly prolonged time spans between ovipositions the more egg batches are produced, which I cannot confirm.

Repeated egg laying itself is not a guarantee for successful reproduction, as many female spiders are known to lay eggs although they never had mated. The case of *Ph.phalangioides* shows that even after repeated egg-sac production the amount of viable offspring can be very high. This is surprising, as the females of *Ph.phalangioides* store the sperm mass in the genital cavity where it is liable to be washed out during oviposition. In fact, only a small amount of sperm seems to be left in the genital cavity, but obviously sufficient to fertilize following egg batches. The remaining sperms are encoiled like the encysted sperm that get transferred in a copulation. From this follows that these sperms are either infertile and not able to capacitate, or that subsequent to oviposition the sperm recoil. The recoiled state might represent a period of reduced energy expenditure, which could increase sperm longevity. In 1985, BROWN demonstrated, that in *Nephila clavipes* the sperm become nonflagellate following oviposition. It is likely that the sperm cells that capacitated prior to oviposition and did not have the chance to fertilize one of the eggs recoil to outlast until the following egg laying. The results show that sperms are able to survive within the secretory substance up to a year (figure 2) and possibly even longer. Therefore, female Daddy-long-legs spiders are not depending on repeated matings to bring forth more than one batch of eggs. FORSTER (1980) developed a hypothetical evolutionary pathway from the "primitive" storage mode where the sperm mass is transferred into and retained within the uterus

externus (bursa copulatrix), to the development of receptacula where the sperm is stored away from the genital tract. FORSTER assumes that the "bursal storage mode" has little survival value. He considers the development of receptacula to be of immense advantage as this would eliminate the need for repeated insemination and would offer the possiblity to economise on the sperm of a single copulation in order to fertilize as many egg batches as possible. Nevertheless, females of *Ph.phalangioides* are able to produce several egg-sacs after a single mating. The claimed negative effect of the bursal storage mode is not that clearcut, but very likely a small percentage of improved reproductive success has been sufficient to stimulate the development of spatially separated storage structures.

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