THE EGG LAYING AND LARVAL DEVELOPMENT OF *PHOLCUS PHALANGIOIDES* (FUESSLIN) (ARANEAE: PHOLCIDAE)

by

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ABSTRACT

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A description is given of the egg-laying of *Pholcus phalangioides* (Fuesslin). The posture of the female, when laying eggs, differs from the resting posture. The eggs appear together with a drop of clear liquid. For a short while the female is kneading this drop after which it is suspended on a thread and spun. After having done so, she takes the egg-batch in her chelicerae and retreats to her resting place. The egg-laying behaviour of *Ph. phalangioides* is compared with that of *Ph. opilionoides* (Schrank) and *Ph. muralicola* Maughan & Fitch.

In captivity the eggs are laid between the end of April and the end of September. A well-fed female lays her first eggs 10-14 days after the first mating. If she has copulated before, the moment of egg-laying is determined by the availability of food. Sperm can be stored by the female. Non-fertilized eggs are removed from the web by the female. The mean number of eggs is 29.8 (7-63). The maximum number of egg-batches is 9. The mean duration of the development until the emergence of the first young is 27.2 days. The duration is temperature-dependent. The female does not hold her eggs continuously in her chelicerae during this period. Ten to fifteen days before hatching the chorions break and the prelarvae are partially visible. The female then starts to loosen the threads around the egg mass and helps the spiderlings to get free. The emerging spiderlings are prenymphs. Their morphology and behaviour are described. The prenymphs moult after 7.9 days, dependent on the temperature.

Key words. — Pholcidae; reproduction; behaviour; development.

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INTRODUCTION

Since 1981 specimens of *Pholcus phalangioides* (Fuesslin) were kept in captivity in order to study their mating behaviour and other aspects of the reproduction.

Hardly anything is known in the literature about egg-laying of this species, although the description of this phenomenon by *Pholcus opilionoides* by Pokrowsky (1899) could refer to *Ph. phalangioides*. Maughan (1978) gives a description of the egg laying with *Ph. muralicola* (Maughan & Fitch). As to the development of eggs and young, additions can be given to the observations published so far.

MATERIAL AND METHODS

The spiders were individually kept in glass cages (20×15×20 cm) with a wooden lid with an opening that can be closed and a larger one, gauze covered, for air. The cages were placed in a room on the south-side of my house. The room has partially a flat roof and a large window. Thanks to this the temperature in the room is strongly dependent on the outdoor temperature. In summertime and in sunshine temperatures higher than 30 °C are reached. In cold weather conditions the room is heated in the daytime but the temperature is rarely higher than 18 °C and falls back to 10 °C at night and in case of severe frost even to 5 °C.

The temperatures mentioned in this study were calculated by means of the monthly survey of the Koninklijk Nederlands Meteorologisch Instituut (Royal Dutch Meteorological Service) at De Bilt (Province of Utrecht), averaging the day-temperatures from Beek (Province of Limburg) and De Bilt.

The spiders were fed with Tipulid midges, Calliphorid and Muscid flies, queens of the ant *Lasius niger* about to take to the air and, in winter time,

with maggots or flies just emerged (Calliphoridae).

Unless stated otherwise, all specimens have been captured at home as adults. Therefore, it was not known if and how often these females already laid eggs before. In the cages mainly females were kept. The males that were put with the female usually stayed with her until their death. Sometimes they were removed after mating.

RESULTS

Egg laying, a case study

The spiders kept in captivity, produced 32 egg-batches, only two of them were produced in the daytime. A description of my only complete observation is given here.

April 21, 1983, 14.45 h. The female hangs upside down in her web. Some time before she starts laying eggs, the abdomen is kept horizontally, but the legs are flexed more strongly than in the normal posture. The tarsi of the corresponding legs are held close to each other, legs I to the front, legs II just above the sternum, legs III just above the epigyne and legs IV more backwards. The tarsi of the legs are all about 0.5 cm apart from the corresponding one in the web.

The female jerks fiercely every now and then with her whole body, alternating with a slow move from left to right, by first tightening the left legs and then the right ones, without shifting the leg position. Again and again she moves her abdomen up and to the front, so that the ventral skin between the epigastric fold and the spinnerets touches a thread kept between the tips of legs III. After that the abdomen is brought back slowly into the horizontal position. This movement strongly resembles the movement the male makes while producing a drop of sperm. All this behaviour of the female is continuously interrupted by spells of total rests.

Then a clear, transparent drop appears from the genital opening in which the white eggs are clearly visible. She holds the drop at the top with legs II and III. It can be seen clearly that she is pressing; at the dorsal side of the abdomen grooves appear in the longitudinal direction. After one minute of pressing the drop is finished and she moves a bit downwards. The drop appears to stick at its top to the thread between legs III. The bottom of the drops rest on the sternum as well as on the abdomen.

The female now begins to move her body backwards and forwards. She holds the drop with her leg II and III, which even sink in it a little bit and seem to stick to it. Light kneading movements are made with legs II and III. It is as if the drop is being massaged. The drop becomes darker in colour. After 4 minutes and about 120 of these kneading movements she stops. The drop now looks greyish and hangs apart from the female loose on a thread, probably the same thread that was first held by legs III. While she holds this thread with the drop with legs II and III, she starts to enswathe it with legs IV. She does this in the same way as wrapping a prey. At first she wraps the lower half of the drop. After 1 minute and 14 seconds she shifts legs II and III upwards along the thread and starts with the upper half. After totally 1 minute and 52 seconds she has spun about 500 threads round the eggs and stops.

During the next 35 seconds the female bites into the bottom of the batch, which she still holds with legs II and III. After this she pivots round her length axis, with the batch in her chelicerae, so that the spot where the batch was attached to the thread, is now below her. Then she lowers herself along the side of the batch and with a quick stroke of her legs she snaps the thread. Next she goes back to a corner of the cage, her resting place, with the egg-batch in her chelicerae (fig. 7). The drop with the eggs still looks greyish and the eggs cannot be distinguished any more.

From the moment of the appearance of the drop till the withdrawal to the corner of the cage, nine minutes have passed. Three quarters of an hour later the drop within the strands of silk has thickend a bit and the eggs are clearly visible as separate globules. The colour of the eggs now is brownish-grey, while being white when appearing in the drop. On June 3rd, 43 days later (in cold weather conditions), 63 young hatched from this egg-batch.

Egg-batches

A. The number of batches per specimen and their spacing in time.

Table 1 shows the dates of egg-laying by the individual spiders, each in its own cage. All batches, except two, were produced at night.

Data per cage.

Cage 0. – In May 1981 a male and a female were put in this cage. During the period in which they were together they repeatedly mated. On October 3 the male ate the female. On November 16 the male died as well.

Cage 1. – On October 5, 1982 a female was put in this cage. On October 26, a male was added, but he was eaten by the female on the same day. On April 14, 1983, again a male was brought in with this female. Mating immediately started, after which the male was removed. The egg-batch of

Table 1. Batches per cage (= spider). Given is the date (day, month, year) and the number of eggs laid on that day (= n).

CAGE	DATE - n	DATE - n	DATE - n	REMARKS
0	21May81-40	01Jul81-12	30Aug81-7	female eaten by male
1	. .	. .	24Aug83-11	no cocoons in '85
	[14May84-*]	. .	[17Aug84-*]	died in April '86
3	?	20Jun84-35	14Aug84-17	2 coc. '85 died Jul85
4	?	17Jun82-30	. .	
	21Apr83-63	30Jun83-46	29Aug83-30	Female died March '85
	[29Apr84-*]	18Jun84-48	05Aug84-32	
5	n.m.	n.m.	18Sep83-17	3 coc. '85 died June '86
6	12Jun83-16	26Jul83-18	01Sep83-17	no cocoons in '85
	15May84-22	. .	06Aug84-25	died October '85
7	04May83-57	26Jul83-18	30Aug83-24	3 cocoons in '85
	16May84-37	11Jul84-26	20Aug84-24	died August '85
9	24May83-41	. .	. .	Also in '84, '85, no coc.
11	04May84-50	04Aug84-46	[11Sept84-12]	2 coc. '85 died Aug.'85

[date-n] = eggs not fertilized and removed by the female.
. . = Female did mate, but laid no eggs.
n.m. = Female did not mate and (thus) laid no eggs.
* = Number of eggs not counted.
? = Female captured whenbeing adult and possibly having laid eggs before.

NB: The female in cage 7 laid eggs in 1985 on May 11, June 30 and August 17. This last batch was not fertilized.

May 14, 1984, appeared to be non-fertilized (solid, yellowish, non globular eggs) and was removed from the web by the female on May 19. The non-fertilized batch of August 17, was sucked by her on August 23, and she removed the remnants the next day. Despite good nourishment she did not produce eggs any more and died the 21st of April 1986.

Cage 3. – On June 18, 1984, a female was put in this cage. This female apparently already mated, no male was introduced.

Cage 4. – On June 8, 1984, a male and a female, captured while they hung in the same web, were put in this cage. On October 20, the weak male was removed. The eggs produced on April 21, 1983, were laid during the afternoon and the description was given above. The eggs still fertile of August 29, were laid 313 days after the removal of the male. A batch laid 577 days later (on April 29, 1984) contained infertile eggs (dark coloured) and was removed by her on May 6. On May 22, 1984, again a male was introduced, mating followed within a few minutes. After recharging his palps with sperm[1]), the male was removed from the cage. In the spring of 1985 she obviously had become very weak, while wrapping prey she inserted long breaks and did not eat them any more. Part of the book lungs appeared to have collapsed or disappeared, while the abdomen had thickened dorsally at the lungs level. She died on March 5, 1985.

Cage 5. – On February 8, 1984, a subadult female was put in this cage. In February she had several maggots for food and moulted to adulthood on April 25. On September 4, 1984, two males were introduced into the cage at the same time. They mated with the female that same afternoon the one after the other. The smaller male was frequently chased by the larger one thus lost a leg and was eaten by this male on October 10.

Cage 6. – On October 25, 1982, a female was put in this cage. On June 2, 1983, a male followed and mating immediately took place. The male died on August 28, 1983. The egg batch of August 6, 1984,

[1]) A male introduced to a female, already has his palps filled with sperm. After courtship and mating, he will recharge his palps within a few hours.

was laid 344 days after the death of the male and contained about 40% infertile eggs. Afterwards the female did not produce any eggs and died on October 4, 1985.

Cage 7. – On November 22, 1982, a female was put in this cage. On April 8, 1983, a male was introduced and again the mating started within a few minutes. On May 16, 1984, she laid eggs round 12.30 hours, an event I just missed. This couple repeatedly mated in the months of July and August. This is the reason why the female lost her egg-batch of August 20 on August 25, when it fell to the bottom of the cage. This female produced three more batches in 1985 and died early October that year.

Cage 9. – A female was put in this cage on October 15, 1982, followed by a male on October 26. The male was eaten by the female on November 2, 1982. In spite of sufficient nourishment she laid no more eggs and died in 1985.

Cage 10. – On October 22, 1982, a subadult female was put in the cage. On May 11, 1983, this female moulted. No male was introduced. In spite of sufficient nourishment she laid no eggs and died in 1985.

Cage 11. – On June 6, 1983, a female was put in this cage. On September 2 a male was introduced and mating started within half a minute. The eggs, laid on September 11, 1984, appeared to be infertile, despite the presence of the (weak) male; they were removed by the female on September 13. The male died on December 19. During 1985 the female laid two more non-fertilized egg-batches and died in August of that year.

If a batch with infertile eggs gets stuck in the web somewhere, after removal by the female, she cuts it loose again until it lies on the bottom of the cage. Sometimes the eggs are sucked out and the remains then removed.

As shown in table 1, the number of eggs can vary strongly from batch to batch. The mean number of eggs was 29.8 (n=27). The mean number of eggs of the batches in the first column is 40.8; these are in general the first batches of the year. In the second column the mean is 31.0 and in the third one, the last batches of the year, the mean is 19.9. Some of the batches are not used (non-fertilized, difficult to place) for calculating these averages. The infertile eggs in batches otherwise normal have been counted.

B. Influence of food on egg-production.

Table 2 shows the time interval between a meal of protein rich prey, such as queens of *Lasius niger* about to fly out, and the production of eggs: an average of 10 days (the female from cage 7 not counted, see table 2). If also other prey animals (smaller flies, midges, Tipulids) are taken into account the mean number of days between consumption and egg-production was 12.6. In February all spiders were fed with one or more maggots or freshly emerged flies.

Table 2. The laying of eggs after consumption of a *Lasius niger* queen.

Date of cons. L. niger	Cage number	Date of egg production	Days later
19 Aug83	1	24Aug83	5
19Aug83	4	29Aug83	10
20Aug83	6	01Sept83	12
19Aug83	7	30Aug83	11
29Sept83	a11	none	—
30Jul84	1	17Aug84	18
30Jul84	3	14Aug84	15
30Jul84	4	05Aug84	6
30Jul84	6	06Aug84	7
30Jul84	7*	20Aug84	21
30Jul84	11	04Aug84	5

* The female in cage 7 still had an egg-batch when consuming a *L. niger*.

The observations described above can be summarized as follows.

In my house *Pholcus phalangioides* produces eggs from the end of April to the end of September and almost always during the night. Only in the case a female is well-fed and mates for the first time, eggs are laid soon after the mating. If a female is less well-fed the eggs are laid only when enough food becomes available.

If a first mating takes place towards the end of the year, the eggs are laid in the following spring. The female of *P. phalangioides* appears to be able to store sperm so that fertilization can still take place 344 days after mating. The amount of sperm received during copulation is sufficient for three egg-batches. After a few days batches only containing infertile eggs are remove from the web by the female.

Food consumption appears to stimulate the production of eggs. Females are able to lay nine egg-batches during the three years they are adult. The mean number of eggs per batch is 29.8. The number of eggs in the first batch of the year usually is larger than in the second batch and lowest in the third batch of the year. Females that did not mate are absolutely unable to produce any eggs.

Table 3. Duration of the development in days of the eggs and the second stage (prenymphs).

A	B	C	D	E	A	B	C	D	E
4	3	30Jun83	16	5	1	1	24Aug83	26	8
7	2	26Jul83	18	6	4	4	29Aug83	28	8
6	2	26Jul83	18	6	9	1	24May83	28	4
3	2	14Aug84	19	10	7	3	30Aug83	30	8
6	5	06Aug84	20	7	6	3	01Sep83	31	9
11	2	04Aug84	20	8	7	4	16May84	36	8
4	7	05Aug84	21	7	6	4	15May84	36	7
7	6	20Aug84	23	12	7	1	04May83	37	8
6	1	12Jun83	23	5	11	1	04May84	39	8
4	6	18Jun84	24	10	5	1	18Sep84	41	14
7	5	11Jul84	24	7	4	2	21Apr83	43	7
3	1	20Jun84	24	9					

A = Cage number; B = egg-batch number of the female concerned; C = date of egg production; D = duration of the development of the eggs in days; E = duration of the development of the prenymphs, in days, till the second moult.

Duration of development of the eggs

All egg-batches studied were laid in 1983 and 1984 by eight females (table 3). The time needed for development in days, from the moment of laying until the hatching of the young, can vary considerably (table 3).

Figure 1 shows the duration of the development of 23 egg-batches put against the mean outdoor temperature during that period. It shows to be strongly temperature-dependent. The mean duration of the development is 27.2 days (S.D. 8.0) with a mean outdoor temperature over this period of 15.5 °C (S.D. 2.7).

Female behaviour while carrying eggs

It was observed regularly that an egg batch carrying female attached it to the web in order to be able to eat, mate or to clean herself, but only a few days after laying the eggs. The female therefore attaches a thread to the web and brings it, with the aid of both legs III, slowly to the batch, the tarsi touching each other. She then takes the batch in her legs II and III and attaches a thread to it by touching the batch a few times with her spinnerets at the point where it is kept by legs III. Then she looses the batch, and by now it is suspended from the web.

A prey can be wrapped by the female while she carries the batch in her chelicerae, but more often she attaches the batch to the web first. If a female carries an egg-batch a male has to exert himself more than usually to obtain a mating, which in most cases meets with success. When a male tries to insert his palps while the female still holds the eggs in her chelicerae, he does not succeed. When after elaborate courtship by the male, the female is willing to mate (the epigyneal region has swollen), she first attaches the batch to the web, mates and then returns to her eggs immediately afterwards. She snaps the supporting lines with her legs III and takes them back into her chelicerae again, sometimes after first having cleaned herself.

When disturbed the female always immediately returns to her eggs and takes them, in case of a serious disturbance, back in her chelicerae, or resumes after a short while, in case of a less serious interference, eating prey, cleaning, but never mating.

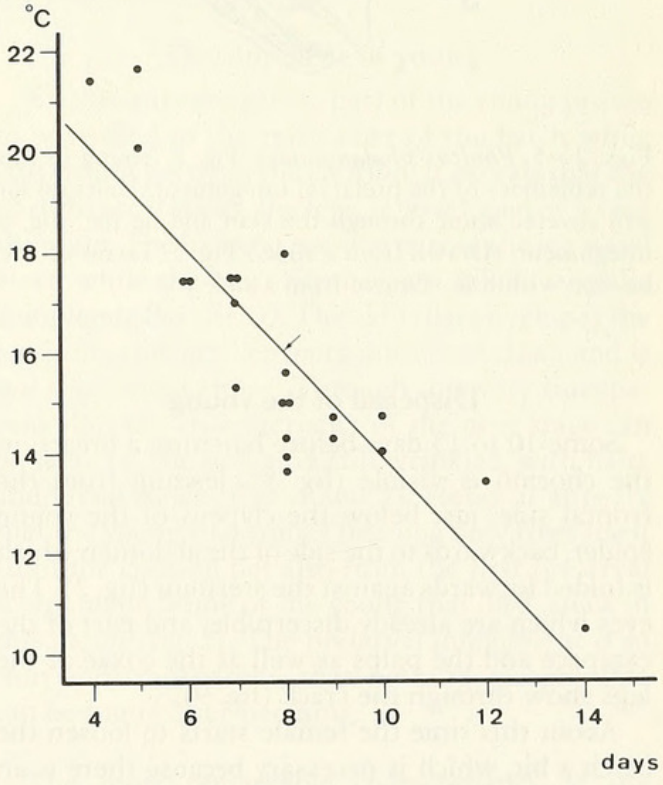
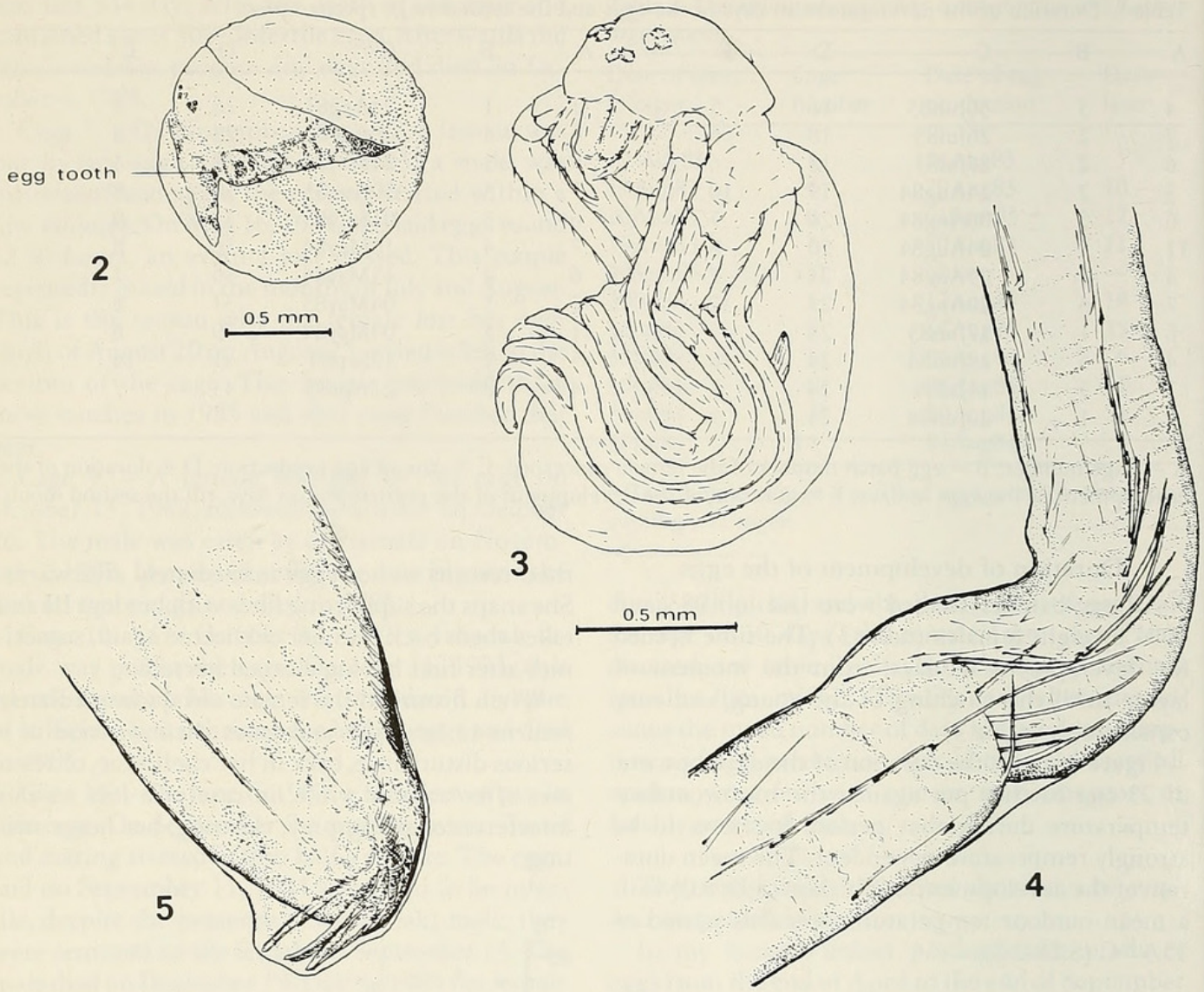


Fig. 1. Duration of the development of eggs in relation to the outdoor temperature. ↓ = indicates the average; ⎯ = linear regression-line: $y = -0.327x + 24.351$; $r = -0.977$; $p << 0.001$; $n = 23$.



Figs. 2—5. *Pholcus phalangioides*. Fig. 2. Young in ruptured chorion. (Drawn from a slide.) Fig. 3. Young stuck in the remainder of the prelarval integument. Hairs no longer covered by the prelarval integument stand erect, others, still covered shine through the skin and lie flat. Fig. 4. Part of a leg (femur-tibia joint) still within the prelarval integument. (Drawn from a slide.) Fig. 5. Tarsus of a leg still within the prelarval integument. The tarsal claws can be seen within it. (Drawn from a slide.)

Dispersal of the young

Some 10 to 15 days before hatching a breach in the chorion is visible (fig. 8), leading from the frontal side, just below the clypeus of the young spider, backwards to the side of the abdomen which is folded forwards against the sternum (fig. 2). The eyes which are already discernible, and part of the carapace and the palps as well as the coxae of the legs show through the crack (fig. 9).

About this time the female starts to loosen the batch a bit, which is necessary because there is an increase in the diameter of the batch (approximately 0.5 mm, as was later measured with other eggs). She does this by biting through the threads round the eggs. She attaches the batch to the web as previously described, holds it with legs II and III with which she turns the batch in order to reach other threads. She then picks up the threads very carefully with the cheliceral fangs without touching the eggs and bites them through or pulls them free. Afterwards she takes the batch in her chelicerae again.

This behaviour was observed 13 days before hatching at the earliest. If she has once started this behaviour, she shows it regularly and with increasing frequency and duration at each bout, as the time of hatching approaches. Towards the time the young hatch, one can perceive a regular indenting of their carapace, just behind the eyes. After a while the spiderling starts stretching its legs and con-

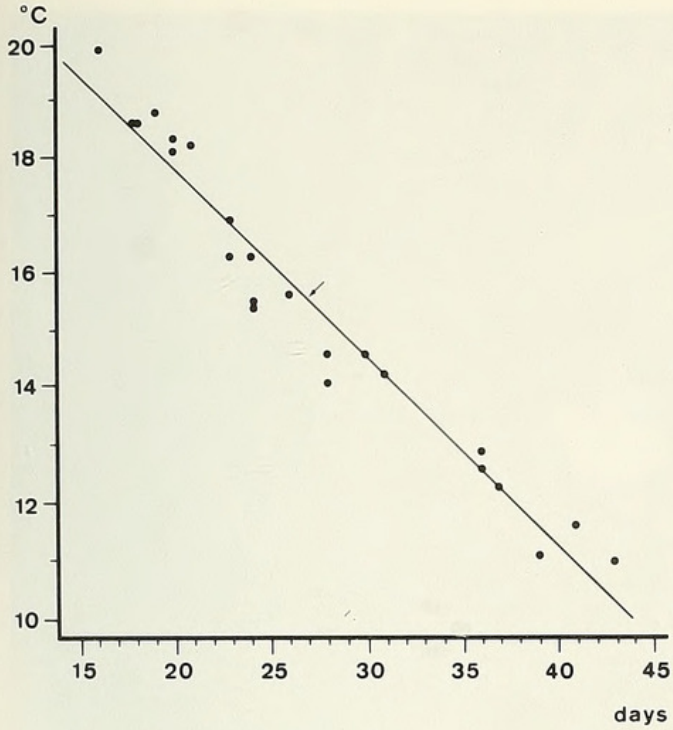


Fig. 6. Number of days between hatching and the second moult (= the first moult outside the chorion), in relation to the outdoor temperature. ↓ = gives the average; __ = linear regression-line; $y = -1.055x + 24.334$ $r = -0.876$: $p << 0.001$; $n = 22$.

tinues to do so until it has freed itself and has reached the outside of the batch. Soon all the spiderlings are on the outside.

Often the female still holds the batch in her chelicerae and after a while she then has a cluster of spiderlings hanging on her jaws (fig. 10). It also occurs that the female attaches the batch to the web when the young are about to emerge or just after the emergence of the first young. Shortly after hatching, till some hours hereafter, the young crawl along the webstrands and disperse just above the remnants of the batch, within a circle with a diameter of about 5 cm, depending on the number of spiderlings. When some spiderlings have remained in the batch, the female is seen to brush the batch, carefully but quickly, with legs II and III and sometimes also legs IV (fig. 12). She also goes on biting the threads, besides carefully evading the bodies of the young spiders. She may be engaged with this behaviour up to three days, with intervals. The young that are still caught in the strands as well as the undeveloped eggs are sucked out, so that only a skin remains, after which she removes the remnants from the web.

As an experiment some batches were filched from the female, at an early stage and not without some effort. They were suspended on a tiny needle in a jar. The eggs developed quite normally, with the exception of a few that were damaged. During hatching it was obvious that those young had great difficulties to free themselves from the spinnings (fig. 11). Even a single thread could give insurmountable troubles. In general the young which were more on the outside succeeded most of the time in freeing themselves after some hours of hard labour. As to the young more to the centre of the batch this effort took much longer. Some of those young did not manage to free themselves even after three to four days of continuous struggle. These young died. Spiderlings near the outside, but caught in the threads with one or more legs, can sometimes free themselves during the first moult outside the chorion. When this does not meet with success they die after all.

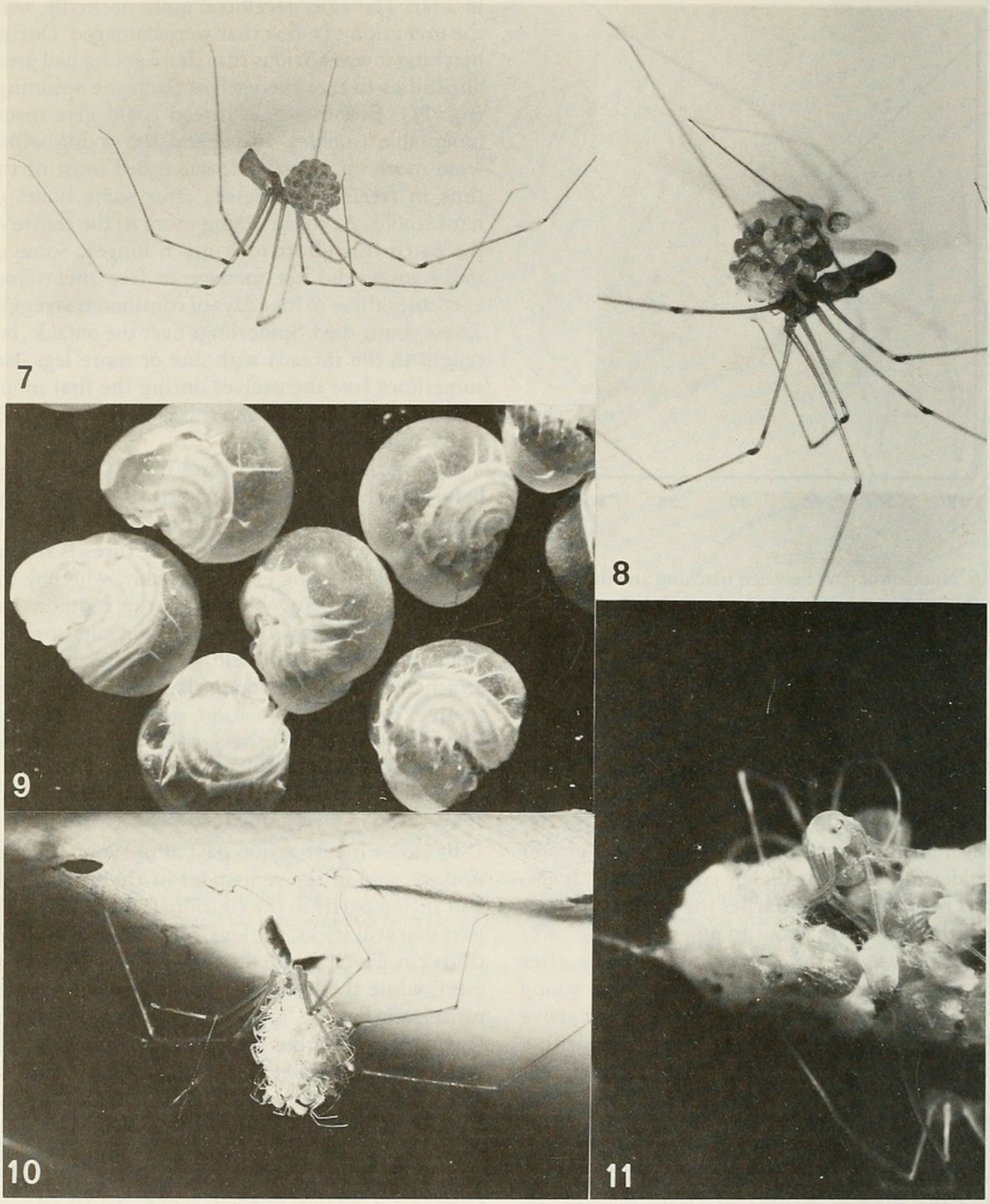
Summarizing we may state that 10 to 16 days before hatching the chorions break. From 13 days onwards before hatching the female loosens the batch more and more by cutting the threads around the eggs. The young emerge quickly, whereby the stragglers are being helped by the mother: she brushes the batch with her legs and cuts threads. The batch is then still held with the chelicerae or attached to the web. Young that stuck are sucked. In an experimental situation, with no female present, the young clearly have more difficulties freeing themselves.

Development of young

By closer investigation part of the young proves to have died in the remainder of the batch while still sitting partly in the chorion. It reveals that the part that still sticks, the legs, is enveloped by a very thin skin. The hairs on the free part of the leg stand erect, while the hairs on the part still covered lie completely flat (fig. 3). The skin that envelopes the legs, contains neither hairs nor tarsal claws and is not segmented either. Through this very transparent skin the characteristics of the next stage can be seen, i.e. the new skin still wrinkled, with hairs and tarsal claws (figs. 4 and 5). Hence it appears that the young that comes free nog only frees itself from the chorion but also from the first prelarval integument. Some of the young that died, stuck in this moult (fig. 3). The prelarval integument is so thin and transparent, that nothing recognizable can be found after hatching.

The most remarkable characteristics of the emerging spiderlings are given below.

Mobility: The spiders move little, disperse inside a small region in the web around the mother and move away when touched.



Figs. 7—11. *Pholcus phalangioides*. Fig. 7. Female with eggs. Fig. 8. Female with loosened batch of eggs, a few days before the dispersal of the young. Fig. 9. Prelarvae after the rupture of the chorion; in the two prelarvae on the left the blackish egg-tooth on the palp is visible. Fig. 10. Female with freshly hatched spiderlings. Fig. 11. A spiderling struggling to get free.

Cuticle: Not pigmented and with fewer hairs than with the nymph.

Legs: all joints are present. Hairs are present, but less than with the nymph. One trichobothrium on each metatarsus. The foot claws are toothed.

Chelicerae: The fang is present and looks nor-

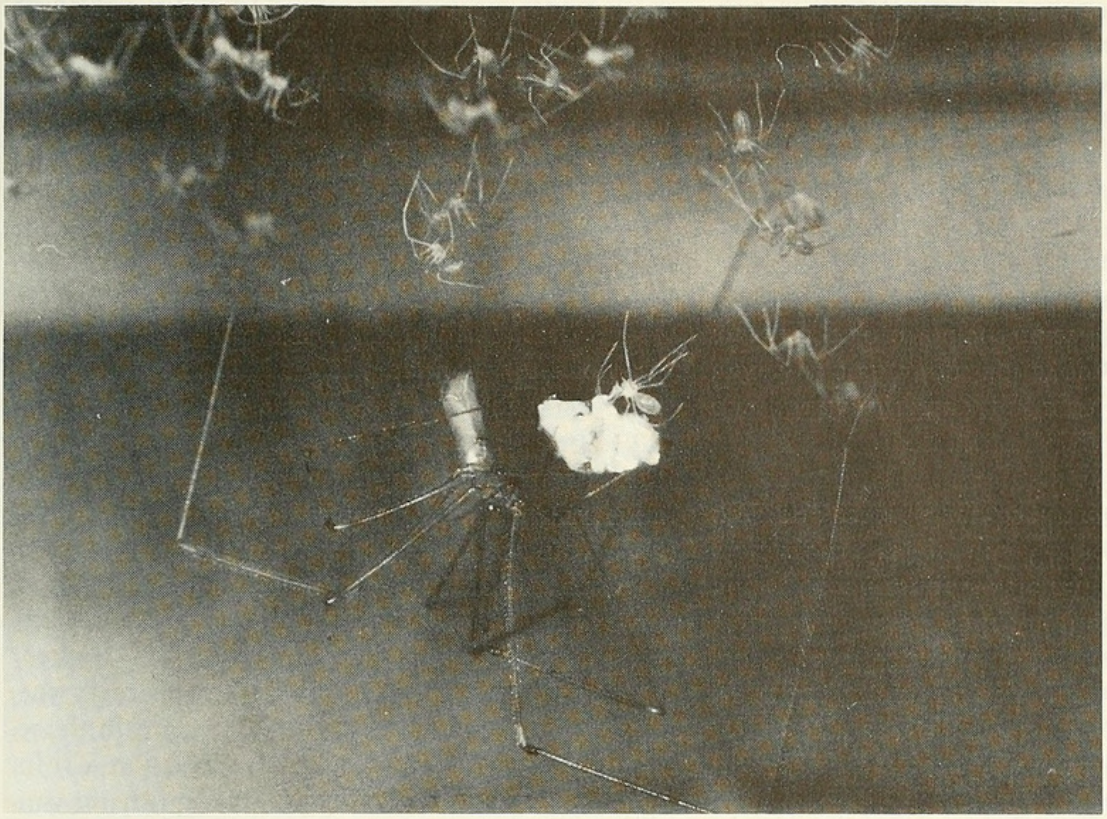


Fig. 12. Female of *Pholcus phlangioides* assisting the spiderlings to free themselves from the webstrands.

mal, but the poison-duct is not clearly visible (a poison-duct is not necessary; they still live on their yolk reserves).

Spinnerets: Spinnerets and silk glands are present. The young are able to spin threads.

Eyes: The eyes look normal, but are surrounded by a brown pigmented area and not by a black area as in older spiders. The eyes are not elevated and lie flat on the carapace.

I have never seen prenymphs spin threads themselves, if they had webstrands of their mother at their disposal (normal situation). I only observed the latter with spiderlings that hatched from eggs suspended from a needle. One day after emergence the spiderlings are able to spin threads themselves. These lines are double and thin and are sometimes drawn out of the spinnerets with the aid of the tarsal claws of legs IV. They are able to attach these lines efficiently, and the fast movements of the spinnerets are then clearly visible. When seriously disturbed they partly drop on a thread spun by themselves. Later they climb back along the same thread. The prenymphs in the mother's web do not yet show the characteristic rapid whirling movements of this family. They pull themselves up a bit between their legs at most, while the mother indeed vehemently whirls. In the first nymphal stage the young do sometimes show this behaviour.

After a period of a few days the young sit very still. When they place the tarsi of the legs close to or against each other the second moult begins.

The time that passes between hatching and this second moult is, as with the development of the eggs, strongly temperature-dependent (fig. 6). On the average moulting starts 7.9 days after hatching (S.D.=2.3; n=22; table 3), with a mean outdoor temperature during this period of 16.0 °C (S.D.=2.7).

A period of 15 days was noted with young that developed in a batch taken away from the female (November 8, 1983).

DISCUSSION

Egg laying, a case study

Egg laying with Pholcids has been described earlier by Pokrowsky (1899) for *Pholcus opilionoides* and by Maughan (1978) for *Ph. muralicola*. Pokrowsky possibly had *Ph. phalangioides* in mind. In the past century these two names were use as synonyms (Simon, 1866). Van Hasselt (1870) also mentioned *Ph. opilionoides* while in view of the size of his specimens he clearly had *Ph. phalangioides* in mind. Nowadays both names are used for different species.

In a few lines Maughan (1978) describes egg laying with *Ph. muralicola*, a species resembling *opilionoides* and *phalangioides* but being a little bit smaller. Both Pokrowsky and Maughan describe the female's posture before laying eggs as a resting posture. They do not mention the tarsi placed close to each other which is not the case in the resting posture. Observations in the literature on egg laying with *Ph. phalangioides* are possible lacking because most of the eggs are not laid in the daytime and the proper laying is only of short duration. Montgomery (1903) "...watched pregnant females for long intervals in the hope of seeing it...", but without success. With *Ph. muralicola* eggs were extruded by pulsating movements of the abdomen (Maughan, 1978). Pokrowsky (1899) describes the female making strange movements with the abdomen extruding the eggs with the aid of abdominal muscles. These movements may correspond with the female's movements observed by me. The action of the abdominal muscles can be seen: the grooves in the longitudinal direction which arise when squeezing. Pholcids do not possess dorsoventral muscles (Kaston, 1981) so that these grooves must be caused by the longitudinal muscles.

The colour of the eggs when laid is in accordance with the observations of Pokrowsky and Maughan. With *Ph. Muralicola* eggs became brown or black as development proceeded (Maughan), while Pokrowsky only describes that the eggs become dry and lose their lustre after a few minutes. Maughan (1978) writes nothing about the presence of a fluid during laying, while Pokrowsky (1899) only mentions that they are "made wet by a fluid". However, I clearly observed a drop in which the eggs appeared. The presence of such a viscid drop was described with more species. In those cases it was observed that the viscosity of the fluid is such that the egg mass largely retains its globular shape. This drop also contains sperms (Gertsch, 1979) or possibly sperms (Montgomery, 1903). The viscosity of the drop with *Ph. phalangioides* is so strong that this, without being wrapped in silk, keeps hanging from a thread all by itself, so that the spider can start throwing silk around it. Assuming that the drop contained sperms, it might be possible that the function of the 4 minutes kneading movements by the female is to produce a better contact of the sperms with the eggs. However, it is also possible that the female checks the viscosity of the drop and waits until this is strong enough by drying up. In doing so the female can leave the drop hanging on a line without the danger of its flowing out and next she can start wrapping it. The former assumption does not exclude the other. The kneading movements were not observed by Pokrowsky and Maughan. Mention is made of the help of legs while laying (legs III, according to Maughan; with one of her legs, according to Pokrowsky). Pokrowsky already saw some threads around the eggs, before the female started enswathing them. In whatever way this is possible is not clear to me. Pokrowsky's observation about the female enswathing the eggs with her front pair of legs must be wrong.

The snapping of the thread on which the egg-batch hangs with the aid of the legs was observed more frequently by me with females that temporarily hung the batch in the web and took it back in the chelicerae after eating, mating or cleaning. Montgomery (1903) also described this behaviour. It is clear by now that *Pholcus* enswathes the eggs with silk. Earlier it was believed that the eggs were merely glued together (Bonizzi, 1869; Becker, 1892), but in what way can the female carry the eggs without damaging them? However, in those days there were authors who did mention a thin silk covering around the eggs (among others: van Hasselt, 1870). Later it was confirmed by more authors (Montgomery, 1903; Bonnet, 1930b; Chrysanthus, 1950; Wiehle, 1953; Bristowe, 1941, 1958; Gertsch, 1979; Kaston, 1981). Carrying the egg-batch in the chelicerae, probably to protect it, is a thing that is mostly mentioned with the descriptions of this species. The silk threads around the eggs are very thin and probably this is the reason why they were not observed by some authors. Yet the number calculated of about 500 lines around the eggs is more than expected.

Egg-batches

The dates for the first batch given in literature are not widely spread. Chrysanthus (1950) saw the first egg-batch on April 26. Montgomery (1903) and Bristowe indicated the month of May for this. The last batches were seen in August (Bristowe, 1958). Montgomery (1903) even saw a female lay eggs in November. However, Schaefer (1976) observed *Ph. phalangioides* laying eggs the whole year through, with a maximum in May. The population investigated by him lived in cellars, where the temperature, in winter, too, did not fall below 20 °C. Schaefer calculated a zero point of development with about 14 °C and also mentioned that females are able either to mate or lay eggs and young are not able to hatch at temperatures below 10 °C. The lower temperatures in winter causes the periodicity found in this and other researches. Bonnet (1930b) in this aspect also mentions; "that spiders do not moult at temperatures lower than

13 °C, one can assume that this temperature at least is necessary, because tissues have to be formed which also applies to the development of the young in the eggs".

Bonnet (1930b) and Schaefer (1976) mention that a condition for the female to lay eggs is that she must have mated, which also appears from this research. Mating does not necessarily have taken place just before laying. Bristowe (1958) already stated that a female is able to produce eggs in May or June, after having mated in the previous summer. Schaefer (1976) mentions a period of 17 to 36 weeks. Now it was even observed that fertile eggs can be laid after a period of 11 months after mating. Some of the eggs in this batch were infertile, probably because of a shortage of (vital) semen. Eggs are laid under good conditions indeed, rather soon after the first mating. This was also observed by Bonnet (1930b) and Chrysanthus (1950). In that case the period between mating and laying is roughly in accordance with the two weeks Seitz (cited in Foelix, 1979) mentions and which are necessary for the increase of the volume of the eggs in the second stage, which starts after mating. An increase in diameter of the female's abdomen was not noticed by me and was not measured either. This again is in accordance with the observations of Gerhardt (1921). Montgomery (1903) and Kaston (1981) wrote that females did not produce more than three cocoons. He probably means: not more than three cocoons per year. It appears that females are able to produce at least six batches with a maximum of nine.

Egg-batches falling on the bottom of the cage only contain infertile eggs in all cases and are removed by the female herself, sometimes after they were first sucked by the female. Van Hasselt (1870) saw up to two times the complete disappearance of a cocoon and then supposed them to be sucked by the female. Montgomery (1903) noticed that from the 12 cocoons observed by him 4 had dropped and did not hatch. He writes that these cocoons dropped by accident when hung in the web. Of the 32 batches observed by me, only one has dropped by accident, apart from the 4 clearly nonfertilized ones, which were removed by the female herself. This was the last egg-batch – in this research – of the female in cage 7. She had to hang the batch in the web many times because of the many matings. On the fifth day after laying she fished up a remainder of an earlier prey in her chelicerae instead of the batch which lay on the bottom. An egg-batch does nog simply fall out of the chelicerae. If one wants to take away the batch from a female, a relatively great force has to be used. It takes a lot of trouble and it will not go without destroying a large number of eggs. Bonizzi (1869) and Montgomery (1903) already stated that the female will not quit the egg-batch even if treated roughly. I assume that the 4 cocoons "lost" by Montgomery's spiders, contained infertile eggs and were removed by the female herself, because none of them produced any young. The egg-batch lost by the female in cage 7, which could be saved, did produce young. Yet a dozen eggs did not survive the fall and treatment afterwards.

A connection between the moment of food consumption and the time of egg production is not mentioned in the literature.

The number of eggs for *Ph. phalangioides* given in the literature lies between 13 and 60 (Bonnet, 1930b; Chrysanthus, 1950; Wiehle, 1953; Kaston, 1981). But these are incidental observations. Only Schaefer (1976) gives a mean number of 33.2 eggs per batch (n = 16, 28-46 eggs).

The diameter of the batches was not measured by me. Locket & Millidge (1951) give about 5 mm for this, and Wiehle (1953) 4 mm. Kaston (1981) even gives the diameter in relation to the number of eggs: a batch of 4.7 mm contained 29 eggs; an other of 3.6 mm had 25 eggs. The size of the eggs was also given by him: 1.2 to 1.3 mm long and 0.94 to 1.2 mm thick. On other cocoons of *Ph. phalangioides* I ascertained later the following diameters and egg numbers: diameter 3.6 mm – 36 eggs; 4.5 mm – 42 eggs; 5.4 mm – 60 eggs. The greater part of the time the first egg-batches are bigger than the next, as with many more spider species that lay eggs more than once (Chrysanthus, 1950; Gertsch, 1979; Foelix, 1979). In addition Gertsch mentions that some of the later eggs may be infertile, owing to the exhaustion of the semen supply stored in the receptacles, and perhaps also to its gradual loss of viability (see also Montgomery, 1908). With *Ph. phalangioides* the latter only seldom happens because the females nearly always are susceptible to the males, this in contrast with the observations of Montgomery (1903) and Gerhardt (1921, on *Ph. opilionoides*). If with *Ph. phalangioides* the male stays away after a copulation, the phenomenon of infertile eggs does occur, but only if afterwards several batches are produced. In general the number of eggs in spring is again larger than the number in the autumn of the previous year, but smaller than in the first batch laid by the female. But as is already mentioned the number of eggs also depends on the supply of food so that differences can also arise because of this.

Duration of development of the eggs

It is only Schaefer (1976) that gives the duration of the development of the eggs in relation to the temperature: 18.1 days with 23 °C (n = 8) and 54.7 days with 16 °C (n = 6). This is in accordance with the data of this research. Other authors only mention the duration of the development observed by them, which most of the time lies between two and three weeks (Bonizzi, 1869; Montgomery, 1903; Bristowe, 1958). Chrysanthus (1950) mentions a very long duration of 52 days for eggs laid in spring.

Female behaviour while carrying eggs

According to most authors the females of *Ph. phalangioides* carry the eggs in their chelicerae from laying up to, or up to and including, the emergence of the young (van Hasselt, 1870; Becker, 1892; Wiehle, 1953; Vachon, 1965; van Katwijk, 1976; Gertsch, 1979; Kaston, 1981; Nentwig, 1985). It was also observed that the female hung the batch in the web, in order to eat, clean herself (Bonizzi, 1869; Montgomery, 1903; Chrysanthus, 1950), or to copulate with an insistent male (Bristowe, 1958). My observations about the way in which the female hangs the eggs in the web and looses them again, is in accordance with Montgomery's observations (1903).

Dispersal of the young

Bonizzi (1869) described the female trying to break the egg shells with her mandibles one day before hatching. He probably observed the breaking of the threads around the eggs. Bonizzi did not observe these threads. For the rest Bonizzi is the only author mentioning this kind of behaviour before the emerging of the young. However, *Ph. phalangioides* starts biting these threads already sooner, probably as soon as the chorions rupture by an increase of volume of the embryo (Bonnet, 1930a; Gertsch, 1979; Foelix, 1979) and with the aid of the sharp egg- teeth at the basis of the palps (Vachon, 1965; Gertsch, 1979). This biting of the threads also occurs with other spiders, particularly wolf-spiders (among others: Montgomery, 1903; Bonnet, 1930a; Foelix, 1979). The fact that females still bite threads after the emergence of the first young, was also observed by Montgomery (1903). This aid appeared to be indispensable for many young. There are clearly individual differences, for some of the females have repeatedly worse results than others.

The time during which the young, after hatching, stay together in a cluster before dispersing in the web to some extent, can vary from some hours (Bonizzi, 1869; Montgomery, 1903) up to some days (Becker, 1892); Chrysanthus, 1950), as also became clear from this research.

Development of the young

The development and morphology of the young of *Ph. phalangioides* after the rupture of the chorion, the presence of a prelarva and a prenymph, are excellently described by Vachon (1965). Emerit (1984 and in a pers. comm., 1985) also emphasizes the presence of a prelarva. The characteristics summed up by me clearly show that the spiderling described is a prenymph (Vachon, 1957, 1965; Emerit, 1984). Canard (1984) uses a different terminology in which these differences with Vachon in relation to *Ph. phalangioides* are given in table 4 (drawn up by Canard, 1985 in a pers. comm.). His terminology shows the different stages in development better, but it is difficult to see when the first period (pullus) ends (with the rupture of the first integument). Accurate observation of the young still partially present in the chorion is necessary.

The duration between the rupture of the chorion and the emergence of the prenymph amounts from 5 tot 10 days according to Vachon (1965), but in this research from 10 to 15 days. Other authors do not mentioned this period, because in general it was assumed that the young did only moult for the first time a few days after hatching.

In the literature the duration of this prenymphal stage is given as 6 to 7 days (Bonnet, 1930b); 10 days (Vachon, 1965) or 7 to 14 days (Bristowe, 1958). Schaefer (1976) again gives the duration in relation to the temperature: 17.3 days with a constant temperature of 16 °C (n = 21) and 7.9 days with a constant temperature of 23 °C (n = 26). In this period the young live on their yolk reserves and are not able to take food themselves (Vachon, 1965), so that the assertion of Bonizzi (1869), that a female spun a fly for them ("...when the more robust of the young animals ran to suck the insects thus prepared for them...") must be questioned. The possibility exists that these "more robust of the young animals" were prenymphs already moulted. A first nymph sometimes carefully tries to suck a prey spun by the female together with her. However, the young was repeatedly spun by the female with the prey. A young that was noticed when sharing in the profit, was simply swept away with a leg each time.

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