Observations on the copulation behaviour of the sheet-web spiders *Linyphia hortensis* SUNDEVALL and *Linyphia triangularis* (CLERCK) (Araneae : Linyphiidae)

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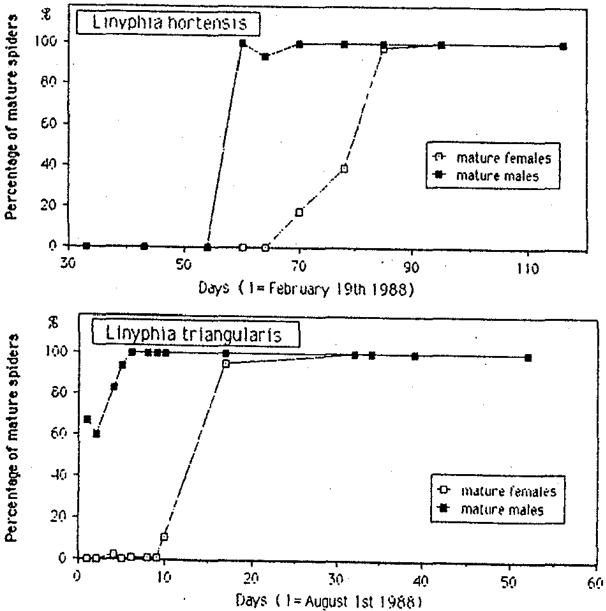
Introduction

Linyphia hortensis and *L. triangularis* are widespread and common palaearctic species of sheet-web spiders (Linyphiidae). Both species have annual life-cycles: while *L. hortensis* matures and reproduces in spring, *L. triangularis* reaches maturity in August and reproduces in autumn. *L. hortensis* hibernates as juvenile (3rd or 4th instar), in *L. triangularis* the eggs overwinter in the cocoon.

L. hortensis preferentially inhabits the upper herb layer of woods or other shady places. *L. triangularis* is common in almost every habitat where a herb or shrub layer is present.

In both species males mature several days earlier than females (**Fig. 1**). After the final moult males leave their webs and begin to search for sexually receptive females. Generally immature females of the pen-ultimate instar are guarded by males for some days (*L. triangularis* : up to 8 days) until they moult. Copulation takes place immediately after the final moult of the females. Often more than one male can be found in the web of a female. In such cases fierce fights between males can be observed. Fights are terminated by the retreat or even the death of one contestant. Copulations are often interrupted by intruding males.

Fig. 1: Linyphia hortensis and Linyphia triangularis . Maturation of spiders near Wuerzburg, Southern Germany, 1988.



Females can mate more than once with the same or different males. In *L. hortensis* experiments with sterile males have shown that second males fertilize on average 21 +/- 22.6 % of the eggs of a female (all clutches, n =23 females).

Mating behaviour in Linyphiid spiders

The mating behaviour was analyzed both in field and under laboratory conditions. Typically the mating sequence can be divided in four distinct behavioural phases:

1 Courtship: The male enters the web of the female. While approaching the female short bursts of vibration alternate with tapping and plucking movements of the forelegs and vertical movements of the palps. The duration of this behavoiur is highly variable and it lasts until the female assumes the mating position and remains motionless.

2 Pseudocopula: The male inserts his palps into the openings of the female epigyne (left palp in left opening, right palp in right opening). The duration of each insertion is short (in both species 3-15 s) and shows little variation whereas the number of insertion is highly variable (*L. hortensis*: 65-120, *L. triangularis*: 200- 500 insertions). During this phase there is no sperm transfer.

3 Sperm-induction: The male leaves the female and builds a small triangular sperm web where he deposits a drop of sperm. The male then dips the tips of his palps in the seminal fluid and absorbs it.

The number of sperm-inductions during a copulation generally is species specific and varies between species (Van Helsdingen1983). In species with more than one sperm-induction these inductions are separated by short series of insertions (**4a**).

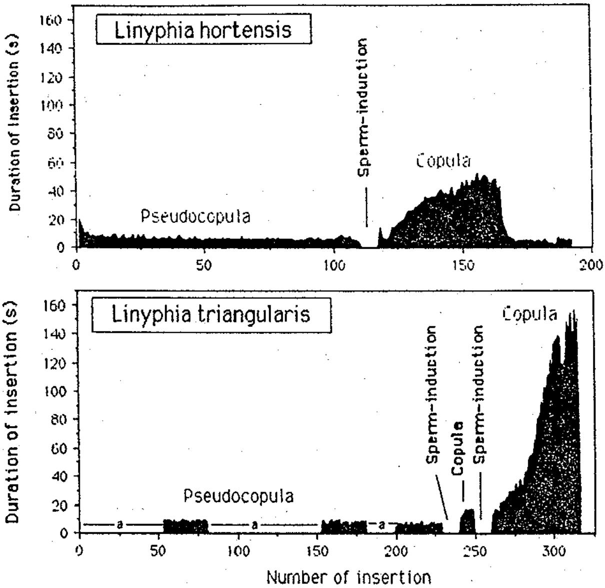
4 Copula: The male continues with palpal insertions (as described under **2**). During this phase the duration of the insertions increases (*L. hortensis*: up to 85 s, *L. triangularis*: up to 180 s). The number of insertions is 45 - 90 in *L. hortensis* and 45-70 in *L. triangularis*..

The typical mating sequences of *L. hortensis* and *L. triangularis* are shown in **Fig. 2** and **Tab. 1**.

Tab. 1: Typical mating sequence in *Linyphia hortensis* and *L. triangularis* under laboratory conditions. (Duration of insertion in min; Mean +/- SD; n: number of different females observed)

Mating behaviour	*Linyphia hortensis*	*Linyphia triangularis*
1 Courtship	2 - 65	5 - 180
2 Pseudocopula	**24 +/- 9.8** (n=286)	**67 +/-18.8** (n=185)
3 Sperm-induction	5 - 10	8 - 15
4a Copula	-----	**4 +/- 1.4** (n=230)
3 Sperm-induction	-----	4 - 6
4 Copula	**37 +/- 8.5** (n=199)	**65 +/-11.4** (n=123)

Fig. 2: *Linyphia hortensis* and *Linyphia triangularis*. Typical mating sequences and duration of insertions. (a: not observed in detail. Each bar represents one insertion.)



Remating probability

Under laboratory conditions the probability that an inseminated female copulates with a second male is in both species significantly higher when the second male is presented immediately (within 6 h) after the first copula (**Tab. 2**).

Tab. 2: *Linyphia hortensis* and *L. triangularis*. Probability for a successful second copulation . (Chi-square test: ** p< 0.01)

Time between mating trials	*Linyphia hortensis*		*Linyphia triangularis*	
	Percentage of successful second copulations			
< 6 h	**65** (n= 122)	**	**24** (n=32)	**
> 24 h	**25** (n=17)		**3** (n=38)	

When the time between mating trials was increased, *L. hortensis* second males broke off a mating sequence more often without sperm transfer after a short period of **pseudocopula** (5 - 10 min).
In *L. triangularis* inseminated females avoided or even aggressively attacked approaching males several hours after the copulation.

If copulations were experimentally interrupted the probability for a second successful copulation increased significantly in both species even if more than 24 h had elapsed between mating trials. Females that were experimentally interrupted during **pseudocopula** or early during **copula** did not differ significantly in their probability to mate with a second male compared to virgin females mating with a first male. If the copulations were interrupted during a later stage remating probability decreased in *L. triangularis* (**Tab. 3**).

<u>Tab. 3:</u> Probability of a successful second copulation for <u>*Linyphia hortensis*</u> and <u>*L. triangularis*</u> females after a completed or an experimentally interrupted first copulation. (Minimum time between mating trials: 24 h; Chi-square test: ** p<0.01)

	Linyphia hortensis			*Linyphia triangularis*	
	Percentage of successful second copulations				
First copulation completed	**25** (n= 17)			**3** (n=38)	
		**			**
First copulation interrupted after:					
a) **Pseudocopula**	**100** (n=10)			**100** (n=10)	
			**		
b) 5-10 min **Copula**	**100** (n=42)			**56** (n=36)	
			**		
c) 20-30 min **Copula**	**100** (n=12)			**9** (n=22)	

<u>The function of a prolonged copula</u>

In the Linyphiid spiders *Frontinella pyramitela* (Austad 1982) and *Linyphia litigiosa* (Watson 1990) sperm transfer takes place during the early part of the **copula**. In *L. hortensis* and *L. triangularis* sperm is transferred during the first third of the **copula.** In *L. triangularis* females even the sperm transferred during the short series of insertions between the two sperm-inductions (**4a** in Tab. 1) can fertilize a considerable proportion of the eggs produced.

Why then do males copulate much longer than is necessary for insemination?

1 Suter & Parkhill (1990) suggest for *Frontinella pyramitela* that the duration of the copulation is positively correlated with the size of the hatchlings in the first clutch. At the present time a similar effect cannot be excluded for *L. hortensis* and *L. triangularis*.

2 In *L. hortensis* the duration of the **pseudocopula** of a second male increased significantly when the **copula** of the first copulation had been completed. If the first copulation was experimentally interrupted during the **copula** the duration of the **pseudocopula** of the second male decreased (Tab. 4). The **copula** of a first male thus seems to have a remarkable effect on the remating probability of a female (already reduced remating probability (Tab. 3), prolongation of the **pseudocopula** of the second male). The mechanism by which this effect is achieved (possible change in the internal structure of the female's epigyne, mating plug, etc.) is not known at the present time, but males thus seem to increase the probability that their sperm will fertilize the female's eggs.

<u>**Tab. 4:**</u> <u>*Linyphia hortensis*</u>. Duration of the **pseudocopula** of the second male. (The duration of a normal undisturbed **pseudocopula** was on average 23 +/- 8.9 min (n= 152). Mann-Whitney-U-test, **: p< 0.01, *: p< 0.05)

		Duration of second **pseudocopula** (min)			
		mean		SD	n
After a completed first copulation		68		25.1	86
First copulation interrupted			**		
after 25 min of **copula**		54		15.3	7
15-20 min of **copula**	*	44		20.4	14
5-10 min of **copula**		34		16.6	51

3 In *L. triangularis* the remating probability increased when the first copulation had been interrupted (Tab. 3). A possible explanation for this might be the existance of a mating plug. During the copulation a drop of a whitish fluid appears in the epigynal openings of the females. After the **copula** this fluid hardens and remains attached to the proximal openings of the epigyne as a plug. The fluid seems to be applied by the males and might serve as a mating plug which impedes further copulations of the female or makes them impossible.

Summary

The mating sequence of the Linyphiid spiders *Linyphia hortensis* and *L. triangularis* were investigated. Under laboratory conditions females of both species copulated more than once . Second males of *L. hortensis* could fertilize on average 21% of the eggs produced by a female. Sperm transfer took place during the first third of the **copula** (copulation phase 4). The prolonged **copula** might impede (*L. hortensis*) or prevent (*L. triangularis*) further copulations of the female. Thus such a behaviour might improve the reproductive success of a male copulating with a virgin female by increasing the probability to fertilize all of the female' eggs.

References

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