

MATING BEHAVIOR OF *THERIDIOSOMA GEMMOSUM* (ARANEAE: THERIDIOSOMATIDAE) - THE UNUSUAL ROLE OF THE MALE DRAGLINE SILK

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Abstract - The mating of *Theridiosoma gemmosum* consists of a series of successive copulations. In the interval between two consecutive copulations, the females unwind the silken threads released by the male spinning organs; these threads are known as draglines or lifelines. The silk thus obtained is rolled up by the females into bundles, which they ingest prior to the next copulation. In other words, the mating of *T. gemmosum* involves the transfer of nutrients from the male to the female via silk. The silk provided by the male during copulation and eaten by the female, can be considered a nuptial gift.

Key words: Spiders, mating behavior, lifelines, nuptial gift, mating plugs

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INTRODUCTION

Spiders of the suborder Araneomorphae, the most abundant in terms of the number of species (see Platnick, 2010), which are also called 'true spiders', are equipped with three pairs of spinnerets, referred to as anterior lateral, posterior median and posterior lateral spinnerets. This is where the spinning glands, located in the opisthosoma, are emptied through sets of jet-like outlets, known as spigots (Foelix, 1996). Thousands of species of this suborder have developed unique ways of using silk, of which only a small number has been sufficiently investigated. Spiders of the superfamily Araneoidea (Griswold et al., 1998), which includes the family Theridiosomatidae, use spinning glands to produce up to seven different protein-based silks/glues that have diverse uses and physical properties (Hayashi et al., 2004; Hardy et al., 2008). Spiders of the family Theridiosomatidae (ray spiders) spin modified orb webs, including, in some cases, three-dimensional orbs. Most of these spiders build their small orb webs with one APR (i.e., above the orb-plane radii) thread that serves as a tension

line (Lopardo and Hormiga, 2006). The spinning apparatus of *Theridiosoma gemmosum* (L. Koch, 1877) was described by Coddington (1986), Scharff and Coddington (1997) and Hajer et al., (2009).

A spider's dragline is also often called its safety line or lifeline (Osaki, 1996, 2003). Used by spiders to build web frames and to drop in a controlled fashion from high places, it exhibits a unique combination of strength and toughness (Tirell, 1996). Anchored to the substratum by attachment discs, the dragline allows the spider to return safely to the starting point after a thrust at prey or following a free fall; it also allows the spiderlings to maintain contact with the parental web (Foelix, 1996).

Dragline silk is an extracellular fibrous protein called spidroin (Leng et al., 2009) produced by the secretory activity of a pair of major ampullate glands, while the material of attachment discs is secreted by piriform glands (Kovoor, 1987). The spigots of both types of glands are located on the surface of the anterior lateral spinnerets.

Male spiders have, in essence, two acts of seminal discharge (Robinson, 1982). They first eject seminal fluid from the genital opening onto a delicate sperm web, from which they then retrieve it with the pedipalps. Later, during the act of copulation, the sperm is again ejaculated, this time from the palp into the female. The indirect method of spider sperm transfer is highly unusual, and spiders tend to have conspicuous and comparatively bizarre methods of courtship and mating (Robinson, 1982).

In adult males, some segments of the palp are modified into a secondary copulatory organ and can either be simple in structure (haplogyne palp) or complex (entelegyne palp) (Jocqué and Dippenaar-Schoeman, 2006). In the entelegyne type of palp the tarsus is usually equipped with a bowl-shaped cavity (cymbium) and a genital bulb. Haplogyne spiders insert the entire bulb of the palp into the female's genital opening; in entelegyne spiders, which include the Theridiosomatidae, only the tip of the bulb enters the copulatory duct. The genital bulb (Figure 2A-B) consists of a more or less sclerotized tegulum which contains a sperm duct, and an embolic division with an intromittent organ called the embolus. The embolus contains the terminal part of the ejaculatory duct and its opening. Another important part of the bulb is the conductor, which runs parallel to and supports the embolus.

The female genital structure in most spider species of the suborder Araneomorphae is made up of a hardened plate called the epigynum (Figure 3A-B) located on the underside of the abdomen in front of the gonopore. During copulation, the palpal organ of the male is inserted into the female's genital opening, and the sperm is deposited in her seminal receptacles. Eggs are fertilized as they pass through the oviducts and out through the gonopore (Foelix, 1996). The force that causes the injection of sperm from the male's pedipalp into the female's receptacle increases blood pressure, expanding the soft vascular tissue known as hematodocha (Figure 6A-B) between the hard plates of the pedipalps (Haupt, 2004). The unusual aspects of spider sexual biology make them extremely promising subjects for future

research of sperm competition and cryptic female choice, and they outline promising lines for future research (Eberhard, 2004).

The research, the results of which are described in this paper, focused primarily on the biology of the very small ray spider *Theridiosoma gemmosum*. As material was collected for the study of the silk and spinning activity (Hajer et al., 2009), a relatively long and unusual mating behavior was observed in the spiders' natural habitat. This behavior was characterized by interrupted copulations, with the males repeatedly running away from the females and subsequently returning. The aim of the research was derived from these preliminary investigations. The main objective was to investigate and describe the courtship and mating behavior in *T. gemmosum*. We were also interested in analyses of female genitalia in order to elucidate whether there exists or not a post-copulatory process.

MATERIALS AND METHODS

Theridiosoma gemmosum is a species whose global distribution covers Europe to Central Asia, and North America (Platnick, 2010). The total length (prosoma + opisthosoma) of adult females is 1.9 to 2.4 mm, while that of males is 1.3 to 1.9 mm (Coddington, 1986). These spiders build their webs (Figure 1) above the water surface in various types of marshy vegetation, such as reed and sedge growth. They are also abundant under overhanging grass on the banks of ditches (Buchar and Růžička, 2002). In webs made by *T. gemmosum*, radial threads (with an embedded sticky spiral, studded with glue droplets) converge in several places, around the center, and gather at the hub, where a tension line gives the entire web a conical shape like an umbrella turned inside-out. The spider stays at the center of the web with its abdomen towards the web (Hajer et al., 2009). Sexually immature specimens were collected from their natural habitat to be observed for their mating behavior and until reaching sexual maturity, they were housed separately, either in small cubic glass boxes measuring $7 \times 7 \times 7$ cm or in larger glass containers measuring $25 \times 8 \times 20$ cm (length \times width \times height)

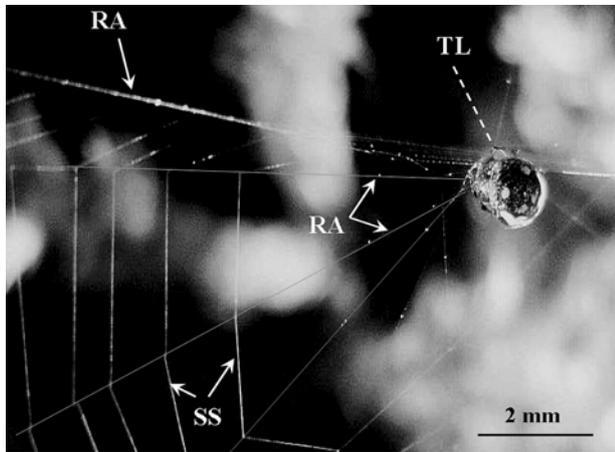


Fig. 1. Central region of an orb-web produced by an adult *Theridiosoma gemmosum* female, side view. The course of the tension line (TL) is highlighted by a broken line. RA – radial threads, SS – sticky spiral, also known as catching spiral.

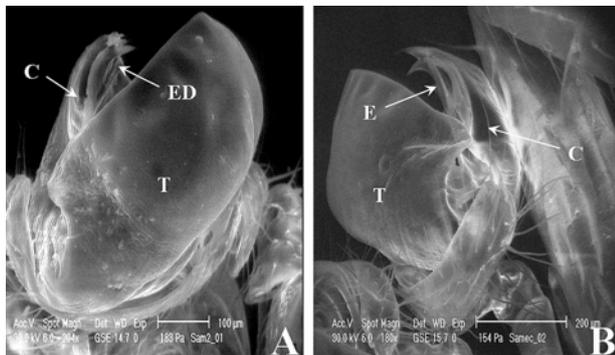


Fig. 2A-B. The male copulatory organ - right male palp, **A** – dorso-lateral, **B** – ventrolateral view. T – tegulum, C – conductor, ED – embolic division, E – embolus.

whose upper walls-cum-lids had holes in them for aeration. Plants of the species *Chlorophytum comosum* (Thunb.) Jacques (common name: spider plant) were placed inside the containers (for details see Hajer et al., 2009). Prior to video recording, adult females were placed in the glass boxes, and once they had built a complete three-dimensional orb-web – which they did invariably within the following 24 h (usually in one night) – adult males were placed in the same containers. Upon reaching sexual maturity, males do not build their own webs intended for prey catching and do not ingest any food. In all cases, vir-

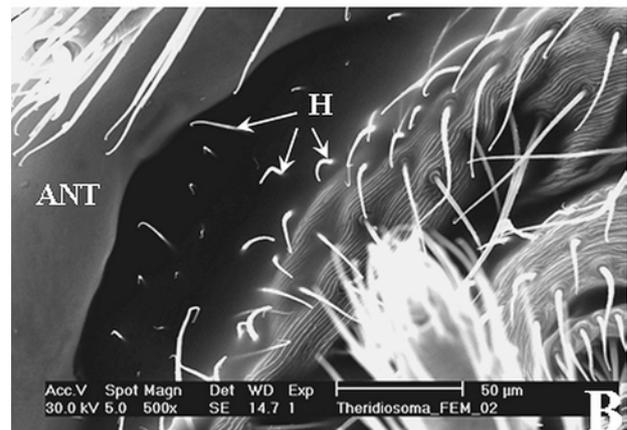
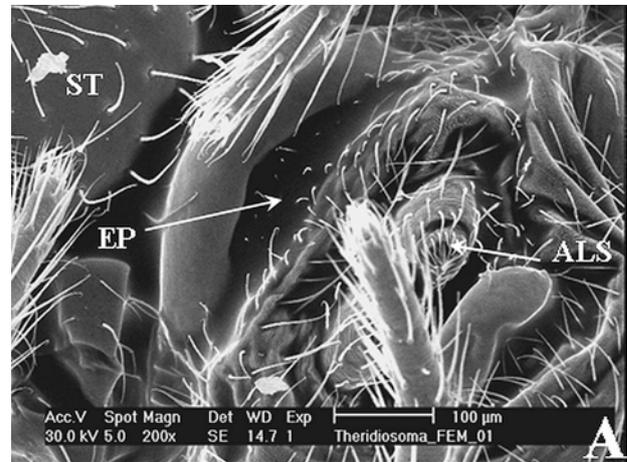


Fig. 3A-B. Copulatory organ of virgin female. **A** – part of the ventral side of the opisthosoma with epigynum – EP. ALS – one of the two anterior lateral spinnerets, the rest of the spinning apparatus is hidden by one of the legs, ST – sternum. **B** – detail of the surface of the epigynum covered in numerous pinnated hairs – H. The epigynum has a noticeably wider anterior edge – ANT.

gin females and males were paired randomly. Observation of the mating behavior was conducted in the summer months (June to September) of 2008 and in May 2009. The temperature in the laboratory ranged between 19 and 23°C (continual temperature measuring was not conducted). Voucher specimens were deposited at the Department of Biology, Faculty of Science, J.E. Purkinje University in Ústí nad Labem, Czech Republic.

An INFINITY LITE digital microscope camera connected to a NOVEX RZT-PL stereo microscope

was used to study the spiders' mating behavior, while INFINITY CAPTURE software was used to process the images and to analyze the videos. For the observation of these very small live spiders, often for several hours at a time, 'cold light' (KVO circular fiber illuminator) had to be used. The number of copulations and their length was measured as the video recordings were replayed. All the video recordings are filed at the Department of Biology, J.E. Purkinje University in Ústí nad Labem, Czech Republic. Images of female and male copulatory organs (Figure 2A-B, 3A-B) were made using an XL 30 ESEM Environmental Scanning Electron Microscope. Use of ESEM did not require any fixation, metal coating or dehydration. Observation under the very low vacuum made possible by this microscope, reduces the risk of undesirable changes to the organisms being observed to a minimum. Fig. 1 was taken using a stereo microscope with a Canon Power Shot S50 camera.

RESULTS

Courtship and mating description

In 29 out of 47 cases (62%) observed in the laboratory, mating took place on the mating lines spun by the males. These threads were stretched between the surface of plants and the hub of the web. In the remaining 18 (38%) cases, mating was observed in the laboratory to take place on the tension line (TL), which is the thread that gives the orb web (Fig. 1) its characteristic conical shape. The mating line itself, i.e. one thread only, is not sufficient for the mating process. Additional threads are always necessary as the males hold on to these during their pumping movements (see below). These can be the threads around the central part of the female web, built by the female during its construction and during the female's movements around the web, or a tangle of threads spun by the male during its movements around the sitting female. However, field observation revealed that the role of the mating line can also be fulfilled by one of the threads in the unfinished female web. In their natural habitat, these spiders build their webs above the water surface in various types of marshy

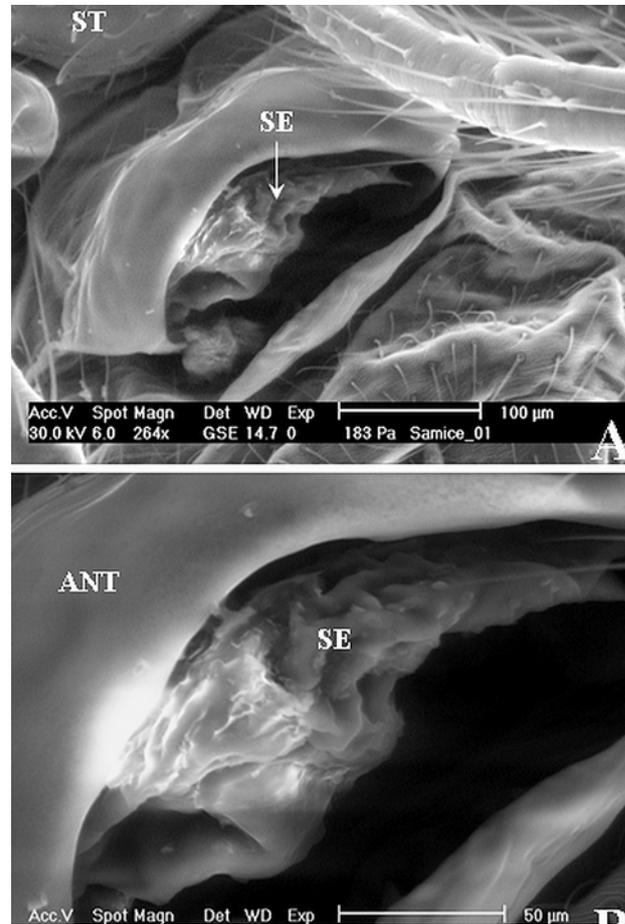


Fig. 4A-B. Copulatory organ of mated female. **A** – overall view, **B** – detail of the secretion accumulated in the epigynum during mating. ST – sternum, SE – secretion, ANT – anterior edge of the epigynum.

vegetation and they tend to become damaged by unfavorable weather conditions (rain, wind). The webs in which copulating spiders were observed in nature often had the appearance of an irregular mesh, where it was impossible to distinguish the threads made by females from those made by males.

Mating is a series of repeated, interrupted copulations and two related, remarkable acts: the production of dragline silk by the copulating males and the ingestion of this silk by the copulating females (Fig. 5A-H). Although the female moves along the mating line towards the male to meet him prior to

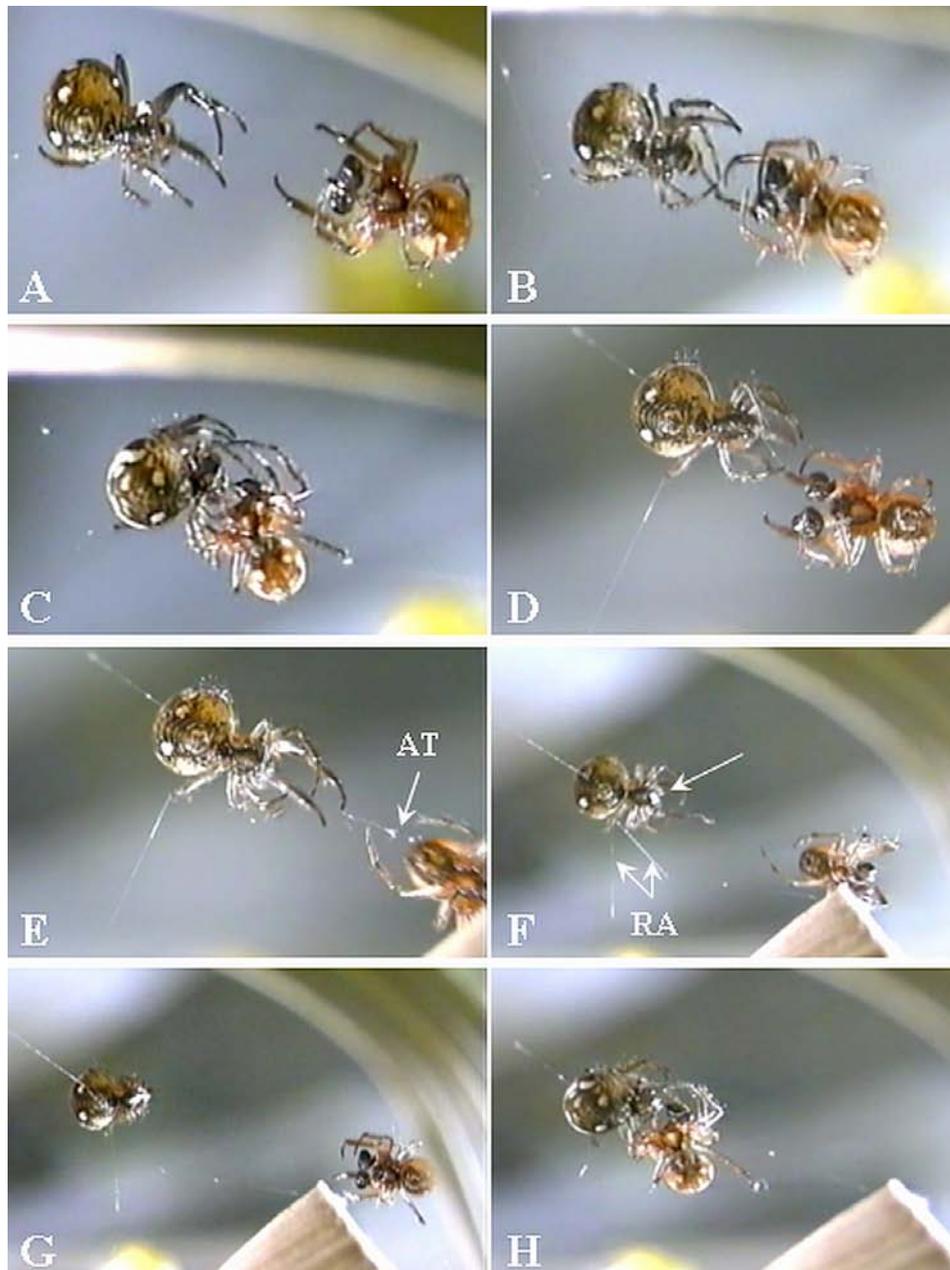


Fig. 5A-H. Eight consecutive acts of mating. **A** – the male (right), hanging on the mating line approaches the female with its back facing down and its first pair of legs stretched out in front of its body. **B** – the first mutual contact with the first pair of legs. **C** – insertion of the male's right palp into the female's epigynum, the beginning of pumping movements (see Fig 6A-B). **D** – interruption of copulation. The male has removed its palp from the epigynum and begins to turn 180° on the mating line so that its opisthosoma faces the female's prosoma. **E** – the male leaves the female releasing a dragline as it does so, and attaches it to the mating line with a small attachment which has the appearance of a tuft of silk. With its first pair of legs the female captures the dragline silk released by the male and begins to bundle it up. **F** – the male stopped at a distance of approx. 12 mm. The males usually remain motionless in this position for several dozen seconds. Meanwhile, the female continues in the active unwinding of the male's silk and gathers it in front of her mouth. The accumulated silk is indicated with an arrow. RA – radial threads (see Fig. 1). **G** – the male has again turned 180 degrees and moves towards the female. **H** – mating continues with another copulation.

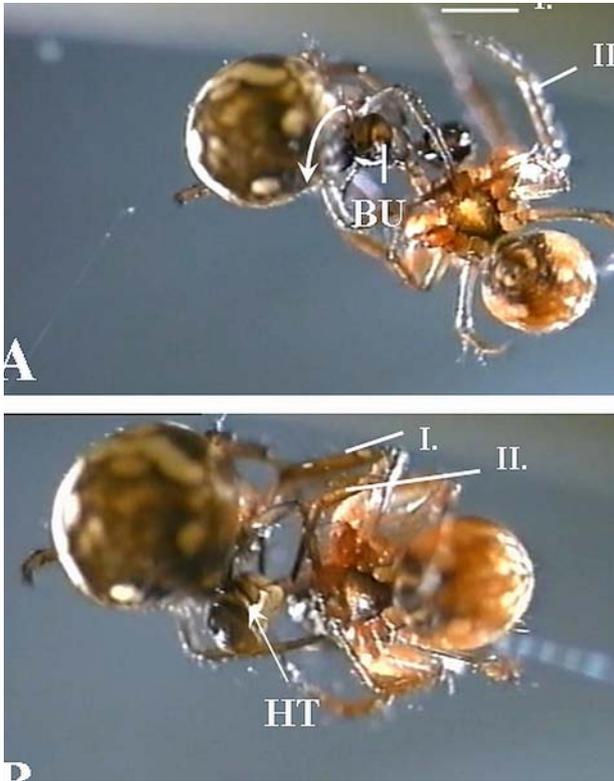


Fig. 6A-B. Pumping movements during copulation. **A** – male with its right palp inserted into the epigynum and its first two pairs of legs (1st and 2nd) outstretched. BU – bulbus. The arrow indicates the movement of the bulbus after the following contraction of the legs. **B** – Male with contracted legs. During this contraction hemolymph is pumped from the body into the bulbus. HT – white hematodochal tissue.

the beginning of mating, i.e. before the first copulation, she remains on the mating line on exactly the same spot throughout the entire subsequent series of copulations. The male, suspended on the mating line, always moves toward the female with its back down and with its first pair of legs stretched in front of its body towards the female (Fig. 5A). The first contact between the male and the female also occurs with the first pair of legs (Fig. 5B). The first and all subsequent copulations begin with the insertion of the embolic division of one of the male palps (Fig. 2A-B) into the female's epigynum (Figs. 3A-B, 5C). The shape of the embolic division, which is supported by a conductor, allows it to become hooked in the female copulatory organ. For a successful insertion,

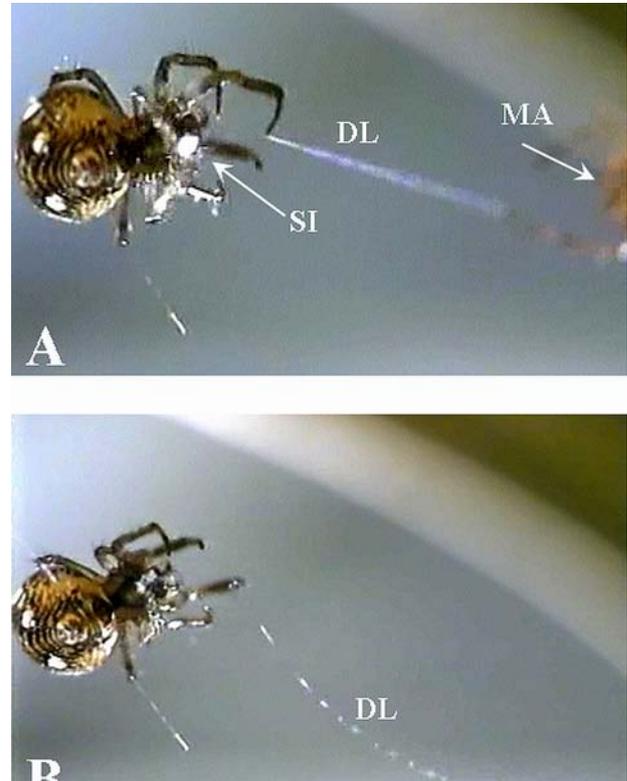


Fig. 7A-B. End of mating after the male stops producing dragline silk. **A** – a female bundles up the male's dragline (DL). A bundle of silk (SI) is accumulated in front of the mouth opening. The arrow indicates the position of the male (MA). **B** – a female ingests the silk and bundles up the remainder of the dragline. She puts the silk into her mouth with the help of the movement of her first two pairs of legs.

the male needs 2 to 3 attempts. The palps are inserted into the epigynum alternately, one at a time. Immediately upon insertion of the palp into the epigynum, the male commences pumping movements (see below), which results not only in repeated erections of the bulb, but also movement (rotation) of the pedipalp in the epigynum. During each interruption of copulation (Fig. 5D), i.e. upon removal of the palp from the epigynum, the male turns on the mating line by 180 degrees (Fig. 5E) and runs away from the female. While doing so, the male trails behind him the dragline he emits, which becomes attached to the mating line by means of the secretion from the piriform glands once the palp is removed from the epigynum. These attachments have the appearance

of white silk tufts. The dragline released by the male is captured by the female at the point of attachment described above, and, using its first pair of legs, the female unwinds it from the male spinning apparatus with a fast movement of the legs. The male stops moving at a distance of 10 to 15 mm from the female. The male remains motionless in this position for between 15–50 sec. (Fig. 5F), while continuing to emit draglines. The male then turns around on the mating line (Fig. 5G), returns to the female and continues with the next copulation (Fig. 5H). The female bundles up the male dragline silk using its front legs, and ingests it at the beginning of the next copulation. The copulatory pattern described above does not change throughout mating.

Unless copulation was disrupted inadvertently during observation and video recording (e.g., by inappropriate handling of the breeding containers, camera or lights), mating lasted (i.e. the time from the beginning of the first insertion until the end of the last insertion) between approx. 42 min 20 s to 126 min 30 s ($n = 23$), the average time being approx. 82 min 20 s. The number of copulations (i.e. the number of insertions of pedipalps into the epigynum) amounted to 16 insertions for the pair with the shortest mating time, as opposed to 48 for the pair with the longest mating time recorded.

As described above, males always insert only one palp at a time into the epigynum during copulation. During these insertions, which ranged in length from approx. 30 s to 6 min 20 s, repeated rhythmic pumping movements take place. While the male holds on to the threads built around the mating line, he repeatedly bends and stretches his first two pairs of legs (Fig. 6A-B). During each of these contractions, hemolymph is pumped into the bulb of the inserted pedipalp, which brings about hematodochal inflations. Conversely, they deflate during the following extension of the legs. At the same time, the bulb, filled with hemolymph and stiffened, makes a slight turn of roughly 90 degrees with each contraction of the legs, returning to its initial position upon their extension. The number of hematodochal inflations/deflations per copulating pair amounted to 54–55 per

min after five minutes; however, it decreased to 32–33 per min after 30 min.

Mating (Fig. 7A-B) ended at the moment when the males stopped releasing dragline silk. Subsequently, the females bundled up the remainder of the dragline and ingested it, while the 'free males' continued moving along the mating line and later moved to the sides of the breeding containers. Those males ($n = 36$) whose mating proceeded and ended as described above (i.e. mating was not interrupted by any external factor) died 2–3 days after mating. Males of the same age ($n = 16$) kept in the laboratory under the same conditions without the opportunity to mate lived 9–12 days longer.

Genitalia and mating plugs

An SEM study of 11 mated females did not find any fragment of the male copulatory organs in their copulatory organ which could be regarded as the reason for the termination of mating. However, certain differences between the epigyna of virgin (EVS) and mated (EMS) females are evident. The cuticle of the EVS (Fig. 3A-B) is virtually smooth, with subtle grooves, its surface – with the exception of the broad front edge – being covered with pinnated hairs. In contrast, the EMS (Fig. 4A-B) is unevenly covered, or rather filled, with a hardened secretion of as yet unknown origin, and hairs are altogether absent or are completely covered with the secretion.

DISCUSSION

The mating behavior of *Theridiosoma gemmosum* was first described by Wiehle (1931) on the basis of the observation of only one copulating pair of spiders. The aforesaid publication also contains information on the process of spinning a sperm web, intended to capture spermatic fluid, and on the process of sperm induction. Wiehle (1931) describes the shape of the spermatic web as forked and the drop of spermatic fluid as 'relatively large'. In a series of copulations lasting approx. 30 min, pedipalps were inserted into the epigynum 13 times; the left palp was used 7 times and the right one 6 times.

The observed male recharged sperm fluid into its palpal bulbs approx. 10 min after the termination of mating, but failed to return to the female. Wiehle (1931) also noted hematodochal pulsations, i.e. alternating inflation and deflation of the white hematodochal tissue and the rhythmic movements of the legs related to these pulsations. The key role of the pumping movements for reaching an erection by means of increasing the pressure of hemolymph inside the copulatory organs was also confirmed by the research presented in this article. In addition to this, it was found that the alternating increase and decrease of pressure of hemolymph in the bulbs inserted into the epigynum, which work like hydraulic organs, causes them to rotate. Although a similar motion has been described for other spider species (Huber, 2004), it has not been observed in *Theridiosoma gemmosum* to date. Spiders of the superfamily Araneoidea are among those spiders whose erection/deflection of the bulb, or the return of the bulb to its original position, is not influenced by the presence of special muscles (Haupt, 2004; Huber, 2004) but exclusively by the pressure of hemolymph.

The mating of *T. gemmosum* was also studied by Gerhardt (1933), who described and drew the position of the male and the female during copulation, measured the mating time for one pair, and counted the number of repeated insertions. The pair observed by Gerhardt stopped mating after approx. 40 min. During that time, thirteen insertions took place; the longest one lasting 5 min 46 s and the shortest one 35 s. After approximately one hour, the male returned to the same female and one more mating took place with two short insertions of a duration of several seconds. However, neither of the above-mentioned authors noticed that the real reason for the interruption and resumption of copulation, or rather the distancing and subsequent coming together of the males and females during mating, is the ingestion of the silk produced by the males. The reason for this can be found in the microscopic technology used at the time, the method of lighting used and the conditions for observation (Wiehle observed the copulating pair in their natural habitat). For a detailed observation of small spider species lasting several hours, not only is it necessary

to use high quality video microscopes, but also 'cold light' (KVO Circular fibre illuminator), which neither Wiehle (1931), nor Gerhardt (1933) used.

The reason why spiders ingest silk is its high nutritional value (Craig, 2003; Miyashita et al., 2004). Dragline silks produced by spiders require more ATP (adenosine triphosphate) than silks produced by larval Lepidoptera (Craig, 2003).

Draglines are recycled by many spiders capable of producing them. The theft of web material is not surprising in view of the web recycling behavior of many araneids (Vollrath, 1987). The mating of *T. gemmosum* involves the transfer of nutrients from the male to the female via silk, in other words, during mating the females recycle the dragline silk of the departing and returning males. In this case nuptial feeding, which improves the fitness of females, consists of silk and not prey items, body parts or even the entire body of the male.

Silk as nuptial gift

Nuptial gift-giving behavior is a rare phenomenon among spiders, being well known among the nursery web spider *Pisaura mirabilis* (Pisauridae) (Austad and Thornhill, 1986; Bilde et al., 2007; Andersen et al., 2008). During courtship, the males of this species offer females prey wrapped in silk (Lang, 1996) which is produced by the secretory activity of the aciniform glands, i.e. the same glands whose fibrous secretions are used by numerous web spinners for 'wrap attacks' to immobilize the prey by wrapping it with a dense silk cover before delivering the paralyzing bite (Griswold et al., 1998; Hajer and Hrubá, 2007). Similar nuptial gift-giving behavior has also been observed in the Neotropical spider *Paratrechalea ornata* (Trechaleidae) (Albo et al., 2009; Albo and Costa, 2010). In the examples given above the captured gift is an insect and aciniform silk is the cover which the recipient female dissolves with the same digestive enzymes used to dissolve the prey.

Like most adult males of the spider species belonging to the superfamily Araneoidea (Griswold et

al., 1998), the adult males of *T. gemmosum* do not ingest any food and in their spinning apparatus they reduce those glands which produce silk intended for catching prey, i.e. for building complete three-dimensional orb-webs (Hajer et al., 2009). Therefore, they do not build webs, do not hunt prey and the amount of energy which they can put into mating is determined by their own fitness. The length of time for which males are capable of producing silk (thus prolonging the series of copulations) undoubtedly depends on their success at hunting for food before they reach sexual maturity, i.e. at the sub-adult stage, when their spinning apparatus is complete.

Does damage to the copulatory organs play a role in the termination of mating?

Copulatory organ breakage, in which a portion of the male's genitalia or the whole palp breaks off during copulation (Knoflach and van Harten, 2001), has not been proven in the case of *Theridiosoma gemmosum*. Broken organs inside the female's genitalia may prevent fertilization by later arriving males, but may also reduce the probability of the male fertilizing additional females (Foelix, 1996). Two important changes in the epigynum of mated *Theridiosoma gemmosum* females are discernible in comparison to the epigynum of virgin females and these are: 1) the presence of a hardened secretion, reminiscent of a so-called mating plug, which can act as a mechanical barrier preventing the resumption of copulation; 2) the absence or loss of pinnated hairs, known as tactile hairs (Foelix, 1996; Barth, 2002) in view of their function, or their covering with the accumulated secretion, which prevents them from fulfilling their role of sense organs.

The production of a mating plug that covers the female genital opening or remains inside the female genital tract after mating is one of many male strategies to prevent or impede a female from mating again. After mating, the males of some species smear the secretion over the epigynum, which prevents the female from mating a second time (Uhl and Busch, 2009). Whether or not the secretion found in the epigynum of mated *Theridiosoma gemmosum* females actually

prevents resumption of mating has not been proven and in this case it appears to be more appropriate to use the term 'mating sign' (Uhl and Bush, 2009). In the more general context of paternity assurance, mating plugs may also prevent the desiccation of sperm, sperm backflow or the discarding of sperm by the female (Eberhard, 2004). Mating plugs mostly consist of secretions that are produced in the male accessory glands and harden in the female genital tracts (Uhl and Bush, 2009). However, the presence of mechanoreceptors or tactile hairs in the epigynum of virgin females is described here for the first time. These small sensory organs are embedded in the exoskeleton at 'strategic' points (Foelix, 1996; Barth, 2002).

The results of the above-mentioned observations justify the use of the term lifelines to describe these threads, like Osaki (1996, 2003), and also confirm the need to investigate them further.

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