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Copulatory behaviour of the goblin spider *Silhouettella loricatula* (Arachnida: Araneae: Oonopidae)

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Summary

Knowledge of the reproductive biology of spiders belonging to the group Haplogynae is very limited. Oonopidae are a diverse haplogyne family systematically placed within the Dysderoidea. The life history of most oonopids is unknown. The present study describes the copulatory behaviour of *Silhouettella loricatula* (Roewer, 1942), a member of the subfamily Gamasomorphinae, including pre- and post-copulatory behaviour, avoidance behaviour, and female aggressive behaviour. Eleven out of 29 females mated in the laboratory and the first-copulations lasted 0.6–1.33 h. Five out of eleven females that had copulated once in the laboratory accepted a second male for copulation. The second-copulations lasted 0.66–1.26 h. Previous studies on *S. loricatula* revealed that females dump sperm of previous males during subsequent matings. The prolonged copulation duration in *S. loricatula* can be best explained by processes involving sperm dumping. In addition, males may perform mate guarding during the long matings. It is suggested that the male palp movements during copulation function as copulatory courtship in order to stimulate the female. Females showed seemingly more aggression during the trials for the second-copulations, indicating that they become less receptive with increasing copulation numbers.

Introduction

According to their genital structures, spiders have been separated into the two groups Entelegynae and Haplogynae (Simon, 1893; Wiehle, 1967; Austad, 1984; Uhl, 2002). Entelegynae are supposed to have more complex female genitalia, whereas a superficial look at haplogyne female genitalia indicates simplicity in form and function (Wiehle, 1967; Uhl, 2002). However, detailed studies have shown that the female genitalia of several haplogynes are in fact highly complex (e.g. Dumitresco & Georgesco, 1983; Uhl, 2000; Huber, 2002, 2006; Burger *et al.*, 2006b, c; Burger & Kropf, 2007; Burger, 2008) and that females of certain species may have direct control over the fate of transferred sperm by, for example, dumping sperm deposited by a previous male during copulation with a subsequent male (Eberhard, 1996, 2004; Burger *et al.*, 2003; Burger, 2007, 2010).

The knowledge of haplogyne reproductive biology is limited to a few members of several families, whereas mating studies on entelegynes have been done for a wider variety of different species (e.g. Bukowski *et al.*, 2001; Clark & Biesiadecki, 2002; Gunnarsson *et al.*, 2004; Uhl *et al.*, 2007). Gerhardt (review in Huber, 1998a) and Bristowe (1929, 1930, 1931) conducted mating studies on haplogynes belonging to the families Filistatidae, Oonopidae, Dysderidae, Segestriidae, Pholcidae, Sicariidae, and Scytodidae. Burger *et al.* (2006a) and Edwards & Edwards (2006) reported on the copulatory behaviour of two tetrablemmid species. The mating behaviour of a member of the oonopid genus *Orchestina* Simon, 1882 was recently described for the first time (Burger *et al.*, 2010). In addition, the most detailed descriptions of reproductive biology and copulatory mechanisms in haplogynes have been given for the family Pholcidae (Uhl, 1993, 1998; Huber, 1994, 1995, 1997, 1998b, 2002; Uhl *et al.*, 1995; Huber & Eberhard, 1997; Yoward, 1998; Senglet, 2001; Peretti *et al.*, 2006).

Oonopidae are a highly diverse haplogyne spider family widespread in many habitats on all continents (except Antarctica) (e.g. Gerhardt, 1933; Harvey, 1987; Saaristo, 2001). They are systematically placed within the group Dysderoidea (Coddington & Levi, 1991; Platnick *et al.*, 1991; Jocqué & Dippenaar-Schoeman, 2007). Based on the classification by Simon (1893) two subgroups are conventionally recognised within Oonopidae and are often treated as subfamilies — the armoured "loricati" or Gamasomorphinae and the soft-bodied "molles" or Oonopinae. Only a small part of the oonopid material currently available has been studied and most genera have yet to be described. Especially the life history of most oonopids is unknown. The diminutive body size (often less than 2 mm) of oonopids and the fact that many species are difficult to collect alive make behavioural observations challenging. The present study aims to describe the mating behaviour of the gamasomorphine oonopid *Silhouettella loricatula* (Roewer, 1942) in detail. In addition, notes on avoidance behaviour and female aggressive behaviour are given. The results are compared with previous findings on mating behaviour of spiders, especially haplogynes.

Material and methods

Specimens: A total of 29 females and 11 males of *Silhouettella loricatula* were collected by M. Burger and C. Kropf from 29–31 March 2003 and 23–26 June 2004 by sieving the humid leaf-litter layer of freestanding carob trees (*Ceratonia siliqua* L.) in Tarragona, Spain. All spiders were mature when collected and thus their mating history was unknown. The spiders were brought to the Natural History Museum of Bern (NMBE), Switzerland and individually kept in the laboratory in plastic boxes (9 × 6.5 × 2.5 cm) with ground gypsum. A small plastic cap (2.5 cm diameter) containing a humid paper towel (5 × 10 cm) was added in each box. The towel was moistened every other day by a few drops of water. The spiders were fed with Collembola (*Folsomia candida* Willem, 1902) and firebrats (*Thermobia domestica* Packard, 1873) once a week.

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Mating behaviour: Copulations were observed with a binocular microscope (Wild M3) and partially photographed using a digital camera (Canon Power Shot G2). For each pairing, the male was carefully removed from his box with a paint-brush and placed into the female's box. This procedure was called a "trial". The spiders were left together for 30–60 min. If no copulation was initiated during that time, the male was put back in his own box and another male was offered after a recovery period of 30 min for the female. When a female copulated for the first time in the laboratory, the copulation was called a "first-copulation". The first palpal insertion by the male was taken as the beginning of copulation. The end of copulation was defined as the moment when the spiders physically separated, which was also the moment when the genital organs decoupled. Post-copulatory behaviour was observed for 15 min in each case. Five females which had copulated once in the laboratory were given the opportunity to mate a second time. One day after a female had copulated for the first time in the laboratory, different males were offered to her one after another (1–2 males per day). When a female copulated for the second time in the laboratory ("second-copulation") no more males were offered and the female was sacrificed immediately after copulation using formaldehyde.

Results

Pre-copulatory behaviour: Approximately half of the females had constructed a web in one corner of the box. It typically consisted of a tube with two opposite openings. The tube was overlaid with long oblique additional threads functioning as signal threads. When a male was placed in the female's box, both spiders usually walked around and appeared to meet each other accidentally. A male which came into contact with the threads of a female's web commenced searching for the female. He usually walked over the web several times and searched for an opening. Except for two cases (see below) the female then reacted by leaving the web and turning towards him. Sometimes the male continued walking around the female and she turned her ventral side towards him by rotating the opisthosoma around its longitudinal axis. No male was ever seen filling his pedipalps with sperm before copulation. In the copulatory position the male was inverted facing in the same direction as the female and seized her opisthosoma with his legs (Fig. 1). When the spiders met frontally, the male grasped the female directly and adopted the copulatory position or he pushed her back and upwards with his front legs. In the latter case both of them palpated each other with the metatarsi and tarsi of their first legs for approximately 4–8 s before the male took the copulatory position by going backwards along the venter of the female. It could not be determined whether the palpating was initiated by the male or the female. When the male approached the female from the side or from behind he jumped at her and gripped her back with his chelicerae. If the female kept running around, the male grasped her opisthosoma with his legs. Before mating, the male crept under her from the side and adopted the copulatory position. In two cases, the copulation took place inside the female's web; the male approached the female from behind and took the copulatory position directly.

Avoidance behaviour: Three types of avoidance behaviour were observed: (i) Sometimes, when put together, the two spiders ran quickly in different directions. (ii) After a male had come into contact with the threads of a female's web and commenced searching for the female, she left the web and walked away. (iii) After having palpated each other with the front legs (once or several times in quick succession), the spiders sometimes walked away from each other.

Female aggressive behaviour: Two distinct types of female aggressive behaviour were observed: (i) When a male approached a female (or if both had already palpated each other with their front legs) she scared him away by vigorous vibrations of her body, and especially of her front legs. Sometimes she gripped the opisthosoma or a leg of the male first. When a male walked over the female's web and came to one of the openings, the female turned towards him and moved her body vigorously. The male then typically went to the other opening. The female immediately turned towards him again and showed the same behaviour. The male usually paced around the two openings of the web 4–6 times before walking away. (ii) When a male had come into contact with a female and tried to creep under her, she turned her opisthosoma away from him and pressed it against the ground. When the male nevertheless managed to grip the opisthosoma of the female and tried to assume the copulatory position, she walked around and pressed her opisthosoma against the ground or pushed her legs IV against his prosoma until he let go.

The females that mated twice did not show any aggressive behaviour during the trials for their first copulations but displayed aggressive behaviour nine times during the trials for their second copulations.

Copulatory behaviour: Eleven out of 29 females accepted a male for copulation (first-copulations). Thirteen trials were necessary to induce these successful first-copulations. The first copulations lasted from 0.6 to 1.33 h (mean=0.79; SD=0.21). Five out of the eleven females that had copulated once were tested to see if they would accept a second male for copulation and all of them did. The second-copulations lasted from 0.66 to 1.26 h (mean=0.96; SD=0.27). The male pedipalps were inserted simultaneously and performed rhythmic movements during the entire copulation. At the beginning the pedipalps were held upright and moved back and forth and/or in circles. One pedipalp started to move first, followed by the other one. Sometimes only one pedipalp moved. The movements performed by one or both pedipalps together changed irregularly. Soon after the beginning of copulation the pedipalps were twisted and only the bent tips of the emboli were inserted (arrows in Fig. 2). The pedipalps then moved in all directions and/or in circles. The movements changed irregularly and were performed by one or both pedipalps together. During the entire copulation, the male moved his body.

At intervals of approximately 10–15 min he pulled his prosoma close to the female's opisthosoma by 3–4 jerky movements followed by about 4–8 quick vibrations of the opisthosoma (arrows in Fig. 3). From time to time the female might take a few steps and slightly change position. About 2–10 min before the end of copulation, both spiders remained motionless. The male sprang away from the female when copulation was finished by turning a somersault.

Post-copulatory behaviour: After their separation, the spiders usually walked away from each other. In some cases, they remained close together and showed intense self-grooming. The male often ran his pedipalps through his chelicerae. No male was ever seen filling his pedi-

palps with sperm after copulation. When the spiders met a second time by walking around after copulation, they usually showed avoidance behaviour (see above). Sometimes the female scared the male away by slight movements of the front legs.

Discussion

Pre-copulatory behaviour: In spiders, the main reasons for a male to court before copulation are probably to avoid being mistaken for prey, to identify himself as a mate of the same species, or to stimulate the female and convince her of his quality (Eberhard, 1985, 1996; Foelix, 1996; Huber, 1996; Huber & Eberhard, 1997;
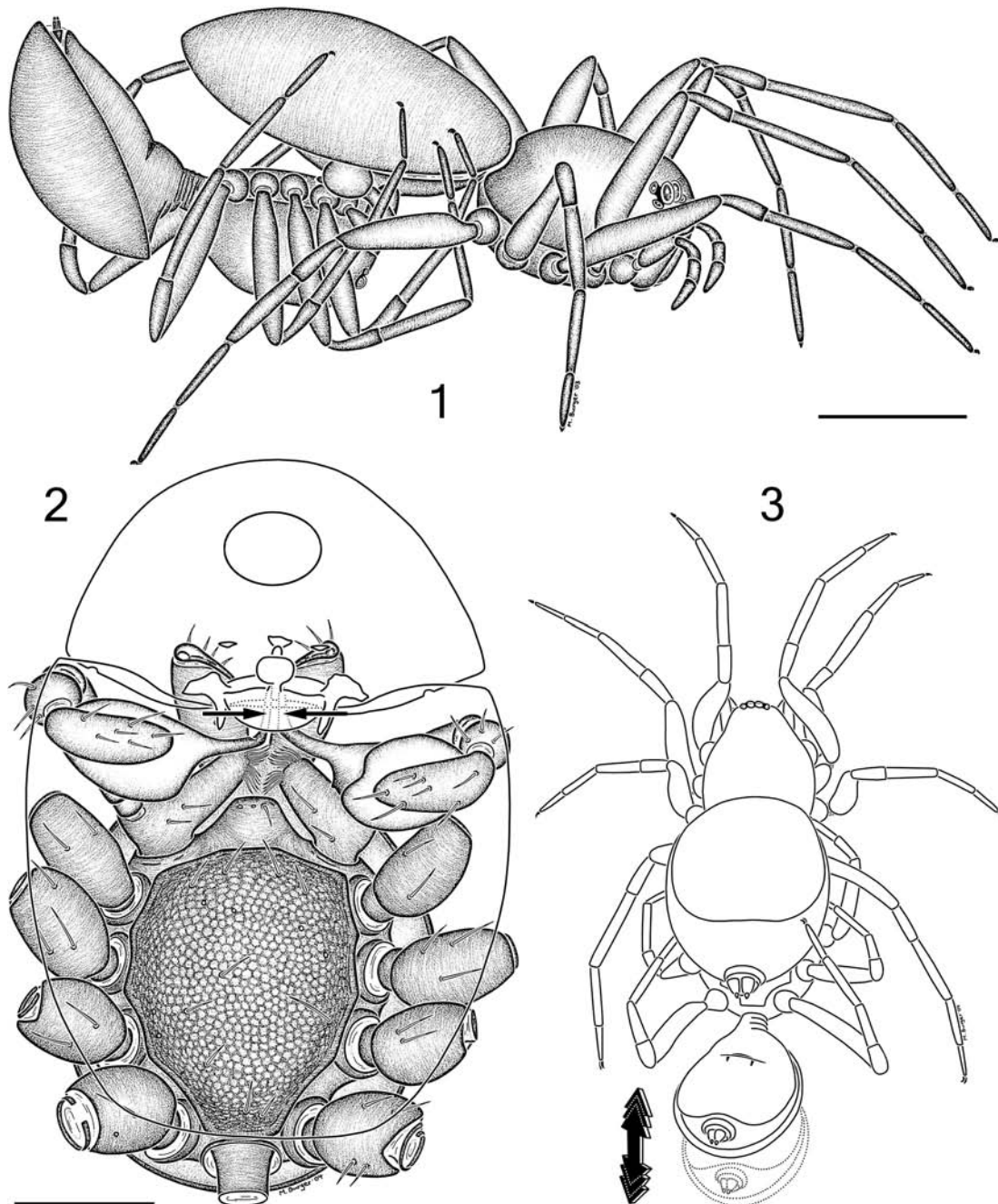
Figs. 1–3: *Silhouettella loricatula* in copula. **1** Pair, male on left, hairs of spiders not shown; **2** Male prosoma, ventral view, legs not shown; scuta of female opisthosoma in optical cut and transparent in dorsal view; arrows point to bent tips of emboli which are inserted simultaneously; **3** Pair, male at bottom; arrows indicate vibrations of male opisthosoma during copulation. Scale lines=0.5 mm (1), 0.2 mm (2).

Bartos, 1998). In many haplogynes the male courtship before copulation is restricted to simple leg and palp movements and abdominal vibrations (Bristowe, 1929; Gerhardt, 1929; Dabelow, 1958; Huber, 1994, 1995, 1998a, 2002; Uhl *et al*., 1995; Huber & Eberhard, 1997; Bartos, 1998; Senglet, 2001). Other forms of male courtship behaviour in haplogynes include tapping or jerking the female's web (Bartos, 1998), cutting threads of the female's web (Uhl *et al*., 1995; Bartos, 1998; Senglet, 2001), or spreading the chelicerae (Jackson & Pollard, 1982). Some male pholcids can even perform gustatorial courtship (Huber, 1996).

In *Silhouettella loricatula*, both spiders palpated each other with the front legs before some matings. This behaviour could have a pre-copulatory courtship function. Similar behaviour has been reported for the tetrablemmid *Indicoblemma lannaianum* Burger, 2005 (Burger *et al*., 2006a), and the oonopines *Oonops placidus* Dalmas, 1916 (Gerhardt, 1930) and *Orchestina* sp. (Burger *et al*., 2010). However, copulations in *S. loricatula* also seemed to take place without pronounced pre-copulatory courtship, as some males just adopted the copulatory position directly. The females which mated twice in the laboratory seemed to show more aggressive behaviour during the trials for their second-copulations. This behaviour could have occurred due to the different mating history of the females. However, the aggressive behaviour of females which copulated twice in the laboratory is an indication of pre-copulatory female choice, as these females often refused to mate with a second male at first but then accepted another male for their second-copulation later. Although the sample size in our study is small, the increase in female aggression during the trials for the second-copulations could indicate that females become choosier with increasing copulation number, as suggested for *Pholcus phalangioides* (Fuesslin, 1775) (Schäfer & Uhl, 2002). Similar female aggressive behaviour in haplogynes has been observed before the copulations of certain pholcids (Huber, 1994, 1995; Huber & Eberhard, 1997; Bartos, 1998), the tetrablemmid *I. lannaianum* (Burger *et al*., 2006a), and the oonopine *Orchestina* sp. (Burger *et al*., 2010).

Copulation duration and copulatory courtship: Copulation duration varies considerably among different spider species (see Elgar, 1995). Some haplogynes copulate for longer than one hour (Gerhardt, 1927, 1928, 1929, 1933; Uhl, 1993; Bartos, 1998; Senglet, 2001; Schäfer & Uhl, 2002; Burger *et al*., 2006a; Edwards & Edwards, 2006). The longest copulation of *Silhouettella loricatula* observed in the present study was a first-copulation lasting 1.33 h. Bristowe (1930) even reported on a mating of *S. loricatula* (sub *Dysderina loricata*) lasting over five hours. It seems obvious that the function of a prolonged copulation in general cannot be explained only by prolonged sperm transfer (Eberhard, 1985, 1996; Suter & Parkhill, 1990), especially since apparent risks are accepted during long copulations (which should favour brief matings), such as increased danger from predators or interruption by another male or the female before sperm transfer is completed (see Eberhard, 1996). Some

studies have shown that there is no correlation between the copulation duration and the amount of sperm transferred (Pitnick *et al*., 1991; see also Eberhard, 1996; Bukowski & Christenson, 1997) and/or fertilisation success (Schäfer & Uhl, 2002), although this might not always be the case (Andrés & Rivera, 2000; Engqvist & Sauer, 2003).

Previous studies on *Silhouettella loricatula* revealed that females enclose the entire ejaculate of the male in a secretion sac inside their receptaculum during copulation (Burger *et al*., 2006b; Burger, 2007) and that the sac is dumped in a subsequent mating (Burger, 2007). It was suggested that the sperm dumping occurs as a result of female muscle contractions in cooperation with the male palp movements which help to discard the sperm of a previous male (Burger, 2007). Based on the female genital morphology sperm dumping was suggested for other oonopids (Burger *et al*., 2003; Burger, 2009, 2010). The prolonged copulation duration in *S. loricatula* can be best explained by processes involving sperm dumping (e.g. the male has to stimulate the female so that she contracts the muscles which leads to sperm dumping). Interestingly, the male palp movements continue after sperm dumping (see Burger, 2007). Together with the vibrations of the male opisthosoma, they indicate that males could perform copulatory courtship in order to induce the female to respond in a way that favours his reproductive success (Eberhard, 1996). Copulatory courtship in the form of palp movements by the male also occurs in pholcids (Gerhardt, 1927; Huber, 1994, 1995, 1998b, 2002; Uhl *et al*., 1995; Huber & Eberhard, 1997; Schäfer & Uhl, 2002).

In addition, the prolonged copulation in *Silhouettella loricatula* could serve as mate guarding. By guarding the female, a male can restrict access to females from other males (Sillén-Tullberg, 1981; Wynn & Vahed, 2004) and consequently guard and protect his own transferred ejaculate (Schöfl & Taborsky, 2002; Linn *et al*., 2007). Suter & Parkhill (1990) proposed that post-insemination mate guarding in the form of prolonged copulation can be expected in species where males are able to displace or dilute sperm deposited by a previous male. Molina & Christenson (2008) showed that previous copulations decrease receptivity of the female and increase her aggressiveness towards a second male in the theridiid spider *Nesticodes rufipes* (Lucas, 1846). This could also be the case in *S. loricatula* since at least increased female aggressive behaviour is indicated by the results of the present study. If males perform copulatory courtship, longer second copulations should result in greater stimulation of the female to receive or use the sperm (Eberhard, 1996).

Copulatory position: Spiders display a wide variety of different copulatory positions (e.g. Gerhardt, 1933; von Helversen, 1976; Foelix, 1996; Huber & Senglet, 1996; Alberti & Michalik, 2004; Gunnarsson *et al*., 2004). The most plesiomorphic copulatory position was defined by von Helversen (1976) as the one taken by most theraphosids (e.g. Gerhardt, 1929; Yáñez *et al*., 1999) and certain haplogynes such as *Segestria bavarica* C. L. Koch, 1843 (Gerhardt, 1929) and *Dysdera crocata* C. L.

Koch, 1838 (Jackson & Pollard, 1982): the male approaches the female frontally, then creeps under her by pushing the female opisthosoma back, and inserts the palps simultaneously or alternately. The plesiomorphic position also occurs in oonopids of the subfamily Oonopinae (von Helversen, 1976). It is taken by members of the genera *Oonops* Templeton, 1835 (Bristowe, 1929; Gerhardt, 1930) and *Orchestina* (Burger *et al.*, 2010). Among different spider groups, a change from the plesiomorphic to a derived copulatory position took place convergently (von Helversen, 1976): the male moves back and both spiders turn their ventral sides toward each other facing in the same direction. The derived position occurs for example in the family Tetrablemmidae (Burger *et al.*, 2006a; Edwards & Edwards, 2006). Within Oonopidae it is adopted by the gamasomorphines *Xestaspis nitida* Simon, 1884 (Gerhardt, 1933) and *Grymeus robertsi* Harvey, 1987 (Harvey, 1987). The present study shows that the derived copulatory position is also adopted by *Silhouettella loricatula* (see also Bristowe, 1930; Burger, 2007).

Acknowledgements

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