

Courtship, mating and agonistic behaviour in *Pisaura mirabilis* (Clerck, 1757)*

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Summary

After a short review of the literature, beginning with the discovery of the nuptial gift of the nursery-web spider *Pisaura mirabilis* (Clerck, 1757) in 1884 by Van Hasselt, the courtship, mating, agonistic behaviour, and peaceful coexistence of a female with two males in a planted terrarium are described (Table 1). Details of the normal mating process with a wrapped fly of different sizes are given (Figs. 3–10). Copulations occurred during both day and night. Eyesight seems to be of little importance for recognition of sexes and the gift, apart from perceiving movements. Mating variations using a freshly caught unwrapped fly (*Lucilia*) (Figs. 11–12), a small fly (one *Drosophila*), a wrapped substitute (heather blossom, Fig. 13) and even without any gift (Figs. 14–15, 23) are shown (Table 4). Males can even perform successfully with females with prey or egg sacs and on nursery webs. Agonistic behaviour, gift robbery, disturbance of mating by a rival, a threesome with one female and two males, but also peaceful male–male encounters are described and illustrated (Figs. 16–23, Table 3). Intersexual aggression and sexual cannibalism are demonstrated and discussed. The so-called “feigning death” of males (Fig. 8) is considered as an evolutionarily stable trick of the male to maintain contact with the female within the dense layer of the herbaceous stratum if she suddenly runs away after a disturbance, or simply for recovering the gift. This behaviour also occurs when two males share one gift (Fig. 22) and try to copulate with each other (Fig. 19). The benefits and disadvantages of the different kinds of gifts, evolution of the gift, its functions and the degree of cannibalism are discussed. Comparisons with the mating behaviour of related Pisauridae and Trechaleidae species using gifts and silk in courtship are made, and suggestions for further research are given.

Introduction

As long ago as 125 years before this paper was written, Van Hasselt (1884: 200–204) described for the first time the nuptial gift of the European nursery-web spider *Pisaura mirabilis* (Clerck, 1757), i.e. prey caught by the male, closely wrapped with silk and transported in his chelicerae, as an “anomaly” among the mating habits of spiders. However, 51 years earlier Sundevall (1833: 199) described males carrying egg sacs in the same manner as females do. Did he misinterpret gifts as egg sacs? In the 20th century many arachnologists, e.g. Lécaillon (1905), Gerhardt (1923: 28–33; 1924: 89–92), Bristowe & Locket (1926: 330–332), Thomas (1928), Nielsen (1932: 135–137), Spassky (1935), Schmidt (1952, 1955, 1980), Leighton (1969), Lierath (1961), Pénicaud (1979: 9, 50–52, 58) and Samm (1994) published their

*This paper is dedicated to A. W. M. van Hasselt (1814–1902), the discoverer of the nuptial gift, Günter Schmidt (1926–), James Carico (1937–2009), and all other scientists studying pisaurids in the past, present and future.

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observations in English, French, German and Russian. Additionally, in recent decades numerous statistically based studies of the mating behaviour of this spider species have been done, and different functions of the gift and its evolution have been discussed (Le Pape, 1974; Austad & Thornhill, 1986; Lang, 1991, 1996; Lang & Klarenberg, 1995, 1997; Schneider & Lubin, 1998; Drengsgaard & Toft, 1999; Pfeil *et al.*, 2001; Stålhandske, 2001a, 2002; Bruun *et al.*, 2004; Prokop, 2006; Bilde *et al.*, 2006, 2007; Hansen *et al.*, 2008; Prokop & Maxwell, 2009). In addition, Vahed (2007) compared the gift of *P. mirabilis* with nuptial gifts of insects. Furthermore, there have been some recent reviews of sex pheromones, intersexual conflict, sexual cannibalism and mate choice in *Pisaura* and other pisaurids (*Dolomedes* species) (Schneider & Lubin, 1998; Prenter *et al.*, 2006; Gaskett, 2007). I checked original papers and secondary literature for descriptions of mating with different kinds of gifts and tabulated them, including also my own results (Nitzsche, 1987: 335). Schmidt (1980: 13, 54–56) also provided a survey about modifications in the courtship and mating of *P. mirabilis*. Moreover, I discovered the origin of prey wrapping by males (immature stages and females show post-immobilisation wrapping of prey as an adaptation to their habitat, the herbaceous layer), and I measured gifts found in the field (Nitzsche, 1981, 1987, 1988). My studies on agonistic behaviour, courtship and the mating process (and prey capture) (Nitzsche, 1981, 1987) have not previously been published in scientific journals, but form part of my monograph (Nitzsche, 1999, 2007) and a popular paper with colour photos (Nitzsche, 2008).

Detailed field studies about the mating behaviour of *P. mirabilis* are still lacking (but for data on reproduction see Pénicaud, 1979; Austad & Thornhill, 1986) and would provide more details about ecology, phenology and reproduction. Nielsen (1932: 137) observed in Jutland (Denmark) some males eagerly courting and females with gifts (15 June 1915 at 10.00 h), but he did not mention any agonistic or aggressive behaviour. Schmidt (1952, 1955) observed the biology of the species both in the field (Lübeck, Schwerin and Rostock in northern Germany) and the laboratory. Pénicaud (1979: 51) noted that matings occurred rarely compared with courtship; he observed the first courtship in Brittany on 8 June 1977, the last on 21 July 1978. Furthermore, A. Loerbrocks (pers. comm.) observed a male pushing his gift into the mouth of a female which was sitting nearly horizontally in the shadow of a leaf.

I wonder why many contemporary scientists (e.g. Stålhandske, 2001a; Bilde *et al.*, 2006; Hansen *et al.*, 2008; Prokop, 2006; Prokop & Maxwell, 2009) did their experiments in containers with smooth walls and paper towels only on the bottom, i.e. under conditions which do not enable the spiders to climb up, contrary to the situation in the field, where *P. mirabilis* is usually found within the herbaceous layer, normally sitting head down on blades of grass lurking for prey. Perhaps it was because of the simpler handling, and may have been inspired by the illustrations of mating on the ground in Bristowe’s well-known book (1958). The horizontal

mating position on the ground is successful, but may produce artificial effects. The ecological context should be taken into account in future laboratory studies, i.e. the spiders should have the opportunity to climb up and rest where they choose. Also, Gerhardt (1923: 21) gave an illustration of mating with the female in the head down position as illustrated herein, but showing incorrect positions of the male's third leg pair and the unused palp, and without showing the male's security thread attached to his gift.

Most gifts found in the field were relatively small and densely wrapped, but with a wide size range between 2.5 and 42.5 mm³, and frequently contain insect larvae (Nitzsche, 1988).

The aims of this paper are: (1) to provide a short overview of the widespread literature in different languages; (2) to present a photographic documentation of the main steps in the courtship and mating with a typical gift as an adaptation to the herbaceous stratum, and to show variations with more or less atypical gifts — small wrapped fly, unwrapped freshly caught fly, heather blossom — and even without gifts; (3) to report for the first time agonistic behaviour, fighting and mating behaviour between two males under semi-natural conditions and in an artificial herbaceous layer; (4) to discuss the senses involved in courtship and mating, the so-called "feigning death", the degree of cannibalism and the functions of the nuptial gift of *P. mirabilis*; and (5) to give a short overview of recently discovered gifts of other pisaurids and trechaleids.

Material and methods

Juvenile and penultimate individuals of *P. mirabilis* were collected in spring and autumn from grass meadows in the western part of Germany (most spiders: Homburg/Saar, 49°18'N, 07°18'E; additional ones: Kaiserslautern, 49°25'N, 07°51'E). They were kept under LD 16:8 conditions (light 05.00–21.00 CET) to increase the rate of development and to overcome the winter diapause (Bonaric, 1980; Nitzsche, 1988). Body length varied, dead males measured 6.5–10.5 mm, females 7.3–14 mm. The spiders were kept individually in plastic vials (5 cm diameter, 10 cm height), containing a bent pasteboard strip stuck on one side at the bottom and a small water-filled bowl, standing with their foam plugs in a water-filled basin to provide the spiders with air humidity (Fig. 1).

Laboratory experiments with male and female

Laboratory experiments were done in spring and autumn between 5 May 1982 and 18 June 1984 (12.00–22.45 CET). Flies (*Drosophila* sp., *Lucilia* sp.) were used as prey for breeding and experiments because of the ease of supply. In their keeping vials (Fig. 1) isolated males were checked daily for carrying of wrapped prey (weak wrapping=only a few threads seen with a hand-lens, obvious=many threads clearly visible, dense=white cover). In one mating experiment a male was put in the keeping vial of a female, and both were checked as often

as possible for mating and cannibalism. In all other cases, first the female and then the male were put into a small glass terrarium (13 × 10 × 10 cm), with movable front cover and moistened blotting paper on the bottom and on three sides; thus the spiders could climb up and be watched at the same time. In the experiments with giftless males heather blossoms were put on the bottom, because heather is a common plant in the north of Germany, where Schmidt (1952, 1955) observed *Pisaura*. Observations lasted from 5 min (unwilling female) up to 181 min (end of copulation, separation of the sexes). The temperature varied between 21.4 and 31.5°C and the relative air humidity between 72 and over 95%. Observed behaviours and times were spoken into a tape recorder, photos were taken with SLR cameras with 100 mm macro lens and electronic flash; additionally some matings were filmed with a video recorder.

Experiments with one female and two marked males

Nineteen males were marked under carbon dioxide narcosis with a unique pattern of up to three spots of acrylic paint on the back of their opisthosoma (Figs. 18, 22). Afterwards they behaved normally. These experiments were done in an artificial habitat, a glass terrarium (30 × 40 × 20 cm) with moistened blotting paper on three sides, strips of adhesive tape crossing the underside of the cover plate, a polystyrene plate on the floor with integrated vertical and oblique strips of wood, and a basin filled with water-saturated foam (Fig. 2). First a female, then simultaneously two marked males were placed in it.

Observations under semi-natural conditions

Additional observations under semi-natural conditions took place in 1980 (27 May–11 June), but were terminated because of egg sac construction by the female (being fed *Lucilia* sp.). In 1998 (12 April–3 August) two males and up to two females together inhabited a glass terrarium (50 × 25 × 30 cm), covered with window panes (two-thirds) and mosquito net, and planted with

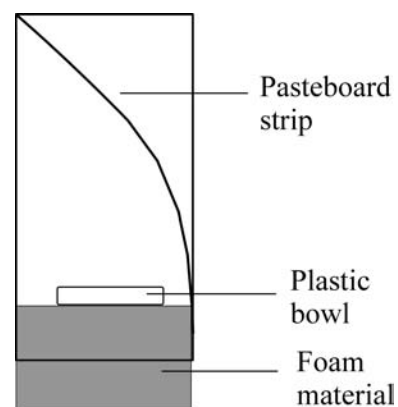


Fig. 1: Keeping vial, a plastic tube (5 cm diameter, 10 cm high), also used for one mating experiment, in the laboratory standing side by side with their foam plugs in a water-filled basin, containing a bent pasteboard strip stuck on one side at the bottom and a small plastic bowl filled with water.

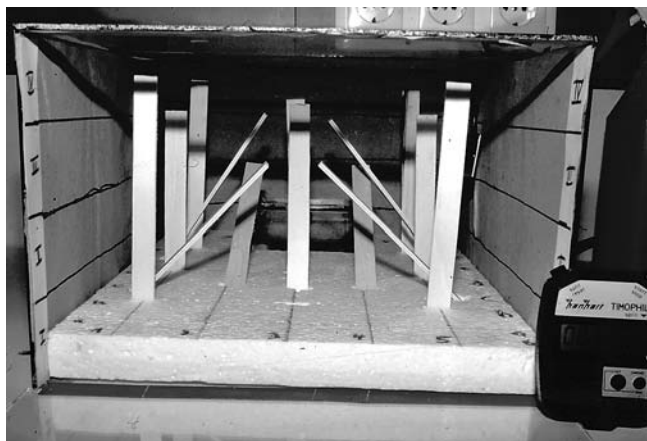


Fig. 2: Artificial habitat used for experiments with one female and two males (glass terrarium, $40.5 \times 30.2 \times 20.7$ cm), with moistened blotting paper on three sides, strips of adhesive tape crossing the underside of the cover plate, a polystyrene plate on the floor with integrated vertical and oblique strips of wood, and a basin filled with water-saturated foam on the floor (photo with frontal glass panel folded down).

spiderwort (*Tradescantia* sp.), between the first day after their final moult until the death of the males or in the case of the females egg sac production or emergence of spiderlings. They were kept under natural light conditions, but at room temperature (and additional lamp above the cage starting with the egg sac period), and were checked irregularly both day and night. Crickets of medium size (*Acheta domesticus* nymphs) were given irregularly in different numbers.

Definitions

Adult age=time since the last moult (absolute in days, relative: 100%=number of days from moult till death); agonistic behaviour=all activities of males relating to a competitor, e.g. threatening, fighting, and fleeing (Foelix, 1996: 200); catching basket=spiders clutching each other with all legs, typical for prey capture behaviour (Nitzsche, 1981: 46–65) and struggles for gifts; male encounters=they touch each other while normally or excitedly walking or show flight or chasing behaviour against the rival, even before any physical contact; double gift=two gifts wrapped together by a male after collecting a second one or winning one from a rival; excitedly walking=males walk with jerks after contact with a female or her silk; feigning death=(a) spider curls all legs under its body and remains motionless, or (b) motionless male, with raised palps and all legs outstretched, remains attached to the gift and is transported by the female or a rival; insertion duration=duration of insertion of one palp, criterion: swelling of haematodochae; copulation duration=sum of all insertion durations during mating; mating duration (holding period in Nitzsche, 1987)=total duration of coupling, from acceptance of the gift by the female until separation of the sexes, including the time when the male may be carried away by her while hanging on the gift, and including short releases of the gift by the female; semi-natural=the spiders lived together in a planted terrarium at room temperature.

Statistical tests (and what used for)

Chi-square test of a cross tabulation (winning of unwrapped versus wrapped fly gift), Kolmogorov–Smirnov test (K–S test) (insertion duration with different gifts), Pearson's chi-square test (agonistic behaviour); in all these tests the calculated value was compared with the table value in Sachs (1978).

Results

1. Observations in the field and under semi-natural conditions

I photographed *P. mirabilis* within the herbaceous layer among blades of grass (Nitzsche, 2008), recorded the cannibalism of immature and penultimate stages, observed a male feeding on a freshly caught small prey item (Nitzsche, 1988: 360), and collected males with gifts which I measured and analysed (Nitzsche, 1988: 358–362). However, I never observed courtship and mating in the field. Therefore, I checked at irregular intervals the sexual behaviour of two males and a female living together in a planted terrarium. In this section the more general observations are given; more detailed results are added to the laboratory data below.

Prey capture, gift size, loss of and searching for gifts

Males and females lurked for prey head down with widespread legs, even on the ground where crickets passed, but the strongest prey-catching reactions, jumping and pursuing, were triggered by flying flies (for analysis see Nitzsche, 1981). Males and females both caught crickets and fed on them, and males produced gifts by wrapping freshly caught prey and prey remains with silk, but they also fed on their gifts. Gift size ranged in length and form from very small spherical (1–1.5 mm in diameter) through oblong shaped ($5 \times 3 \times 3$ mm) to long and narrow, such as a wrapped cricket leg ($8 \times 1 \times 1$ mm). Also a 20 mm long cricket was caught by a male; he fed on it, but probably could not produce a gift of it because of its enormous size and his inability to cut it up. Males searched for lost gifts by moving in circles and feeling with their front legs up and down, normally after a struggle with a rival, but also after the winning of the gift by the female at the end of mating and once after disturbance by the observer. Sometimes gifts fell down and were lost while still hanging on a thread attached to the leaves.

First male and female encounter

After contact with the place where a female (adult age: 1 day) had been sitting just before, a male (adult age: 4 days) showed sexual excitement. Afterwards he produced a very small gift (1–1.5 mm in diameter, content unknown) and offered it. Mating took place in the afternoon, but was terminated by a cricket which came in contact with the female's legs: the female ran away and the pair separated. New offerings of this gift occurred. Later in the evening the male wrapped a

freshly caught small cricket, thus producing an oval gift ($3 \times 1.5 \times 1.5$ mm), and fed on it at some distance from the female.

Activity during day and night

Not only during the day but also at night I observed lurking with widespread legs for passing prey, prey capture by males and females, gift production, feeding, spinning of sperm webs and sperm induction (between 10.10 and 23.50 h), searching behaviour for lost gifts and prey remains, normal and excited walking with and without gifts (between 09.17 and 23.44 h), and grooming activities of males after fixing their gifts by some threads to the substrate.

Aggression and peaceful coexistence

One case of cannibalism occurred: a young female caught a smaller female at midnight and fed on it. Only one aggression of a female against a male was observed: in the morning he followed the female's dragline, she quickly turned around, and he jumped away. Once a feeding female was observed beating with her right legs I and II against a gift-offering male; later she accepted his gift. Sometimes females fled from the gift-offering males: they walked away and hid on the ground or behind leaves; this occurred several hours after moulting to adult, or when probably satiated (with fat opisthosoma), and a few hours before egg sac production. Thus, most aggressive encounters took place between males (see below).

Mating

Table 1 shows some observed features of mating. Males offered their gifts to feeding or preyless females, and even those with egg sacs or on nursery-webs. They used wrapped prey items as gifts in all 33 copulations. Mating took place during both day and night, and females accepted gifts and mated for the first time one day after their last moult. Females mated up to three

Observed copulations	<i>n</i>	%
With gift*	33	100
Without a gift	0	0
Total	33	100
Female mated:	<i>n</i>	day
First time (after final moult)	–	1 or 2
Per day	1–3	–
Until first egg sac	7–8	–
Last time before egg sac	–	1
After first discarded egg sac	2	–
On nursery	3	–

Table 1: Observed matings of *Pisaura mirabilis* under semi-natural conditions (two males and up to two females within a planted terrarium, checked visually as often as possible). *Wrapped cricket, prey remains or unknown contents. Earliest/latest observed insertion: <04.43–? a.m./11.59–00.26 CET.

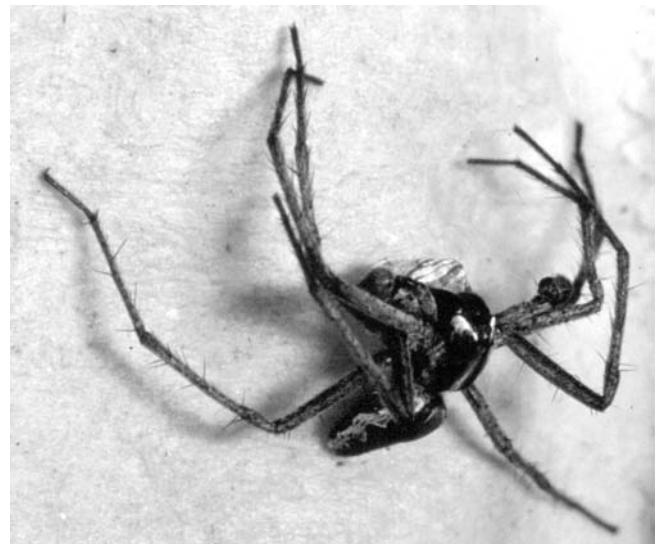


Fig. 3: Male of *Pisaura mirabilis* offering his gift below the female and simultaneously rubbing his legs together (I–III left, I–II right).

times per day (but usually only once), and up to a total of eight times before producing the first egg sac. Sometimes the male did not succeed in inserting his palp or tried to do so on the back of the female; later, insertion of the same palp was successful. Insertions were terminated by the male or the female. At the end either the male or the female won the gift (usually the male).

2. Analysis of courtship and mating in the laboratory

Normal procedure: Male offers closely wrapped prey

Males of *P. mirabilis* produce gifts in an endogenous way (Leighton, 1969), not only when triggered by the presence of females. When isolated in their keeping vials (Fig. 1), they eat their first prey items after maturing. Three-day-old males may carry weakly wrapped prey; they produce white (densely wrapped) gifts from the sixth day onwards (for details see Nitzsche, 1981: 93–100). Isolated males carry their gifts for up to 9 days (for details see Nitzsche, 1987: 87–89).

Finding female and sexual excitement: Most males spin their first sperm webs within four days after their final moult (see Nitzsche, 1987: 92–93). With gift and sperm in their bulbs, ready for mating, they search for females. There seems to be no visual recognition of females, because males may pass resting females in well illuminated environments, and courtship and mating also take place at night. Males recognise females by their chemotactile sense: they stop in places where females have been sitting shortly before. Five different kinds of excitement may follow: (1) palpal tremor, (2) shivering of the opisthosoma, (3) jerks of the whole body at a frequency of 1.3 Hz, then (4) they follow with jerky steps tasting the female's dragline with front legs and palps until they touch the female. However, (5) the most striking kind of excitement is "leg rubbing": distal parts (tibia, metatarsus, and tarsus) of legs I–III of one or both sides or in other combinations are simultaneously rubbed against each other with fast movements (Fig. 3).

The last behaviour occurs during locomotion and while presenting the gift below the female, but also without a gift. It alternates with motionless offering of the gift or new wrapping and is not specific for courtship, because males without excitement, penultimate stages and females also rub their legs together when grooming, but for significantly shorter periods than excited males (for details see Nitzsche, 1987: 106–108). The female normally does not show any excitement, but sometimes her opisthosoma trembles slightly. All these vibrations caused by excited males are transferred to the substrate, i.e. blades of grass or herbs (or blotting paper in the experiments), and may be recognised by the female.

Offering gift, acceptance, and the four phases of mating: The male offers his gift with the prosoma lifted, and with his palps and first legs stretched sideways, thus presenting it in an optimal way for the head-down resting female, i.e. there is nothing between her and the gift (Fig. 4). Alternatively to this passive form of offering the male may walk over the female and stroke or beat her with his first pair of legs. This behaviour seldom occurred in gift-carrying males (but was recorded in a male with a small gift); more often it was observed in giftless males (see below). The female either does not show any reaction, or she may stretch the first leg pair ahead. He continues to offer his gift, rubs his legs or even rewraps a white gift. If interested, she slowly feels for the male by moving her first and second pairs of legs up and down. Feeling his front legs, she is guided to the raised gift in the centre. Sometimes she may come in direct leg contact with the gift (Fig. 4), but in most cases she touches only the prosoma, palps or legs I–III of the male. Just a moment after her now outstretched palps have touched the gift, she bites it and starts feeding. Females took 39 s (mean: 39.2 ± 22.9 SD, range: 14.5–77, $n=10$) from the start of feeling the male up to biting the gift. The time until acceptance may be delayed if some of the male's legs are positioned between the pair of spiders or if the male beats on the female with his front legs. For example, feeling lasted 133 s after a bite in a male's leg. The process is shortened when a more



Fig. 4: Female of *Pisaura mirabilis* (right) feeling for the gift offered by the male. Note the female's right leg II in contact with the gift, left leg I in contact with the male.



Fig. 5: A female of *Pisaura mirabilis* head down, with a darker coloured male below her with raised palps, both sexes biting the gift, a wrapped fly (*Lucilia*).

active male brings his gift into contact with tarsus I of a motionless female, sitting with outstretched legs: she wakes up and bites the gift. The shortest way, which seldom occurs, is when she bites the gift in a prey-catching manner (see Nitzsche, 1981: 147).

The mating proceeds in four phases: (1) The female and male form a gift-coupled pair, the female in the normal head-down position, the male below her head upwards with raised body and palps (Fig. 5). In this phase she immediately starts feeding on the gift while he stays motionless. His palps may tremble slightly, sinking slowly down and being raised again and again.

(2) In the second phase the male becomes active: he suddenly begins jerking strongly, thus shaking the female which lifts up to three pairs of her legs from the substrate, positioning them vertically close to her body; this enables easy access for him to her epigyne on the underside of her opisthosoma. The shaking male curves the end of his opisthosoma inwards, loosens his chelicerae from the gift and fixes a dragline on it. Then he places his third leg pair on each side of the gift and climbs up, either on the right or left side of the gift and female. Then his right or left palp feels for her epigyne. He inserts one embolus, while the tip of his unused palp stays in contact with the gift.

(3) Thus, now and during the ensuing insertion the male secures his gift from four sides: by his dragline, both legs III and the uninserted palp (Fig. 6). His chelicerae are positioned near the gift, ready to bite it immediately, if the female suddenly moves. In this quiet third phase, while the female is feeding on the gift, the male inserts one embolus; when on a vertical wall (as in the experiments) the pair hang supported by from only one or up to five legs. His haematodochae change from expanding to contracting, thus rotating the embolus into her epigyne. The measured duration of one insertion varied from under one second to more than 58 min (mean: 6 min 45 s \pm 11 min 26 s SD, range: 1 s–58 min 26 s, $n=585$, different kinds of gifts). The surface of the closely wrapped gift where the female is feeding changes

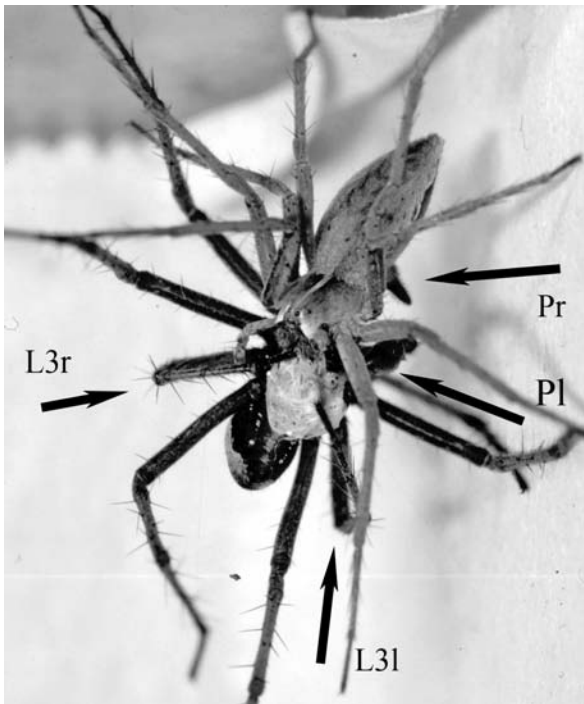


Fig. 6: Mating of *Pisaura mirabilis* (female sitting head down, male upside down relative to her on her underside), insertion of right palp (Pr) on her right side, while she is feeding on the gift (dark area). Note the position of the male's third legs (L3r, L3l), his dragline and left palp (Pl); they all are in contact with the gift, and his right leg III is not far from her fangs.

in colour from white to black, but the silk is not damaged (Nitzsche, 1988: 365–370). She slowly turns the gift with her palps, thus changing and enlarging the feeding area, and sometimes causing one of the male's third legs (e.g. right leg III in Fig. 6) to come close to her chelicerae and perhaps get bitten, but in most cases he withdraws the leg before a bite can occur.

(4) The male then leaves the underside of the female and bites the gift again: male and female thus form a gift-coupled pair again (phase 1, Fig. 5). After a break the male tries to insert the other palp in the same way as described. Further insertions may follow.

Separation and gift winning: In most cases the female forms a catching basket and wins the gift. The male may also react in the same way, forming a catching basket and biting the gift again (Fig. 7). Thereby both may lose contact with the substrate and fall down to the ground, where they separate, one having won the gift. In other cases the female may suddenly run away, while the male is still inserting, and she thus wins the gift. However, if the male bites the gift quickly enough, he may be carried away by her while hanging on to the gift; his legs are outstretched and his palps raised (Fig. 8). As soon as the female rests again and continues feeding, he “awakes” from his motionless posture and tries to insert again (phase 2). In other cases she simply performs a jerky movement sideways, causing the inserting male to lose contact with the gift and fall to the ground. Sometimes the male wins the gift by grasping it in the same way as females do. Especially in matings with small gifts, I recorded bites or attempted bites by the female on leg III or even the body of the male, causing separation or even

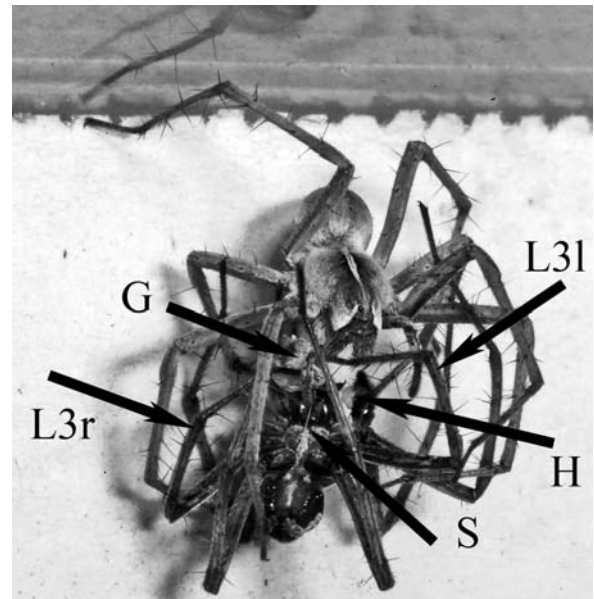


Fig. 7: Struggle for possession of a small gift consisting of one wrapped fruit fly (*Drosophila* sp.). Female *Pisaura mirabilis* (above) has terminated the male's insertion by forming a typical catching-basket with her first three pairs of legs in order to win the gift; the male (below) with bent legs is also biting his gift. Note the still swollen haematodochae of his left palp (H), the security thread between his spinnerets and the gift (S) and his incurved right leg III (L3r) touching the middle of the gift (G). At this moment, both male and female are only attached to the substrate by her last pair of legs and security thread; therefore pairs often crashed to the ground during separation.

the death of the male (Fig. 9). However, separation of the sexes may also occur peacefully: the male simply cedes his gift to the female. In 67.5% of all experiments with different kinds of gifts the female won it at the end of mating, and fed on it leaving only inedible remains ($n=151$, male: 24.5%, male and female: 6.6%, lost: 1.3%, details see Nitzsche, 1987: 148–158). For SEM photos of

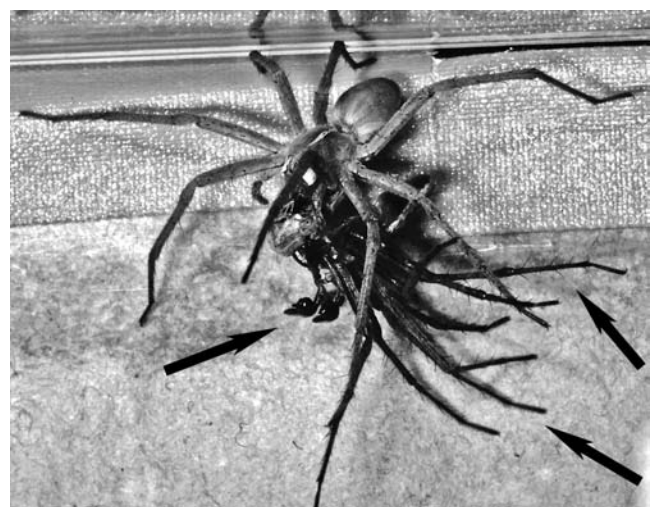


Fig. 8: Female of *Pisaura mirabilis* sitting head down with the gift in her fangs and the male hanging on it below. She has just walked a few steps dragging the male hanging on the gift with her. Note his raised palps (left arrow) and compare with a male carried by another male (Fig. 22). Note also the outstretched legs (right arrows) of the so-called “feigning death” posture of the male and compare this with the appearance of a dead male in Fig. 9.

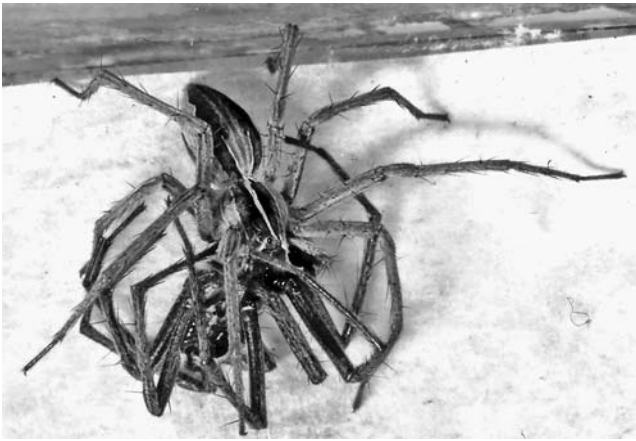


Fig. 9: *Pisaura mirabilis* female with a freshly killed male. The gift was small, only one wrapped fruit fly (*Drosophila* sp.), but was accepted by her, and short insertions occurred before her attack. Note bent legs of the male, unlike the outstretched legs and palps in Fig. 8. Compare with a similar situation of another mating with the same type and size of gift where only the gift was bitten by both female and male (Fig. 7).

the gift surface before, during and after feeding see Nitzsche (1988). If the male retains his gift, he attaches it to the substrate, then he grooms his legs and palps (Fig. 10). Later he may spin a sperm web, feed on his gift, wrap it again and offer it to the same or another female.

Mating variations with different types of gifts

Freshly caught unwrapped fly: When a male catches a fly in the presence of a female, he usually wraps it, thus producing a typical gift. However, males may also offer freshly caught flies, still twitching or wriggling their legs,



Fig. 10: Male of *Pisaura mirabilis* grooming his right leg III after a successful mating, separation and winning his gift. Did the female bite him? Note the dark part of the gift where the female has fed a few moments before.



Fig. 11: Both male (below) with raised palps and female of *Pisaura mirabilis* biting an unwrapped fly (*Lucilia*). Note one wing of the fly covers the female's genital region (arrow).

and females accept them at once (Fig. 11). Frequently females show typical prey capture behaviour, probably triggered by the movements of the fly. I observed successful insertions, but one wing of the fly may lie over the female's epigyne. This impedes the male in copulation or misleads him, so that he walks around the fly instead of to the underside of the female (Fig. 12) and takes longer before inserting. The insertions with unwrapped *Lucilia* flies were relatively short, only 2.5 min (median, for further data see Table 4). The female won the fly in most cases (59%); the male never regained the whole unwrapped fly because the fly often broke into two parts, one for the female and the other for the male. This split occurred significantly more frequently with unwrapped flies than with wrapped ones (compare data in Table 4, $\chi^2 = 13.521, p < 0.001$).

Small wrapped fly: In the laboratory, males catch prey items of different kinds and sizes, even small fruit flies (*Drosophila*), and spin them together. The mating procedure with a single wrapped (or unwrapped) fruit fly may also be successful (Fig. 7) but, because of the small gift size, the male's third legs lie directly in front of the female's mouth. Several times I observed a female chewing on the male's third leg and even on his uninserted palp, resulting in the end of insertion and separation of the pair. Once, a female bit a male's leg, but released it after the end of insertion and kept the gift, thus he was wounded, but still alive. It is astonishing that the sexes struggle for possession of such a small gift. Insertions lasted 1:49 min (median, further data in Table 4), and females seldom produced offspring.

Wrapped heather blossom substitute: Males without gifts in the presence of females try to catch prey, and if



Fig. 12: Mating of *Pisaura mirabilis* with an unwrapped fly (*Lucilia* sp.). Note the unusual position of the male (right) hanging at some distance from the female on the large fly instead of on her underside, and his insertion attempts with his left palp on the fly (arrow).

there are movements, even of the female, they will lurk with widespread legs or show typical searching behaviour: they walk around with their mouthparts close to the ground, feeling with their front leg pairs and palps. During their search they may jump on and form a catching basket around any moving object, even if bumped by their own legs. The first contact with a heather blossom lying on the ground was usually made by a leg I tarsus, followed by the palps. When drawn to the mouth it may or may not be bitten by the chelicerae. Males felt or grasped blossoms relatively frequently, but they carried them or wrapped them near the female less frequently (Table 2). In 20 experiments (Fig. 13) 16 males contacted blossoms, but only six of them wrapped the blossoms, producing gifts. However, four females accepted these gifts, and in two cases the insertions were successful in producing offspring; other females mated without gifts (see below). Insertions with

Heather blossom	Mean \pm SD	<i>n</i> Min-max
Male contact	6.4 \pm 5.6	1-24
Transport	1.3 \pm 1.4	1-5
Wrapping	0.4 \pm 0.5	0-1
Accepted by female	0.2 \pm 0.4	0-1

Table 2: Frequency (number of times by each male) of heather blossom gift production and acceptance by *Pisaura mirabilis* ($n=16$ experiments with heather contact, four different males mated, for mating information see Table 4).

heather blossom lasted 7:51 min (median, for further data see Table 4). Females often released the gift (1-10 times, mean: 3.8 ± 4.3). Note that females won these vegetable gifts (with male's silk) in the majority of cases.

I observed a female biting a male's left leg III during one insertion; he drew it back, and his third legs were then no longer in contact with the gift, so that the female easily won the wrapped heather blossom at the end. Females had problems in fixing their chelicerae in the dry, hard surface of the blossom beneath the silken cover. Sometimes males, having dropped blossoms, kept heather *stalks* in their chelicerae, and at first carried but then dropped them also ($n=4$). On two occasions a male carrying a blossom grasped a further blossom, but dropped it at once and the first one as well. Once, a heather twig was attached to a wrapped blossom during mating and was added to by the male after separation by further wrapping (photo see Nitzsche, 1988: fig. 11c). Twice a female was observed biting a blossom while feeling down to the male, but dropped it at once as the male approached, then the male jumped to the blossom and bit it without accepting it.

Courtship without a gift: What happens if a giftless male encounters a female? Perhaps he has not caught anything, he may have eaten his prey, or a rival may have robbed him of his gift (see below). He walks around searching for slowly moving prey or prey remains, or lies in wait for faster moving or flying insects such as crickets or flies. If there are blossoms on the ground, he may make one into a gift (see above). Virgin females will allow insertions without gifts (43.8%, $n=16$). The male shows the typical sexual excitement. The female walks downwards, moving her front legs up and down, towards a giftless male who is in the typical offering position (cf. Fig. 4 with gift). On one occasion a female bit the right leg III of a male, but a giftless male usually evades bites by walking away or beating the female with his front legs. The female then stops walking and may run away, but usually she sits with her first leg pairs folded and her body pressed to the substrate (Fig. 14). Some females are active: they may suddenly raise their front legs or jerk. After such a jerk one female rubbed legs III and IV over her epigyne (function unknown); a short time later she suddenly raised her right legs I and II, causing him to recoil and walk away. Males usually stop feeling, take a step back or run away

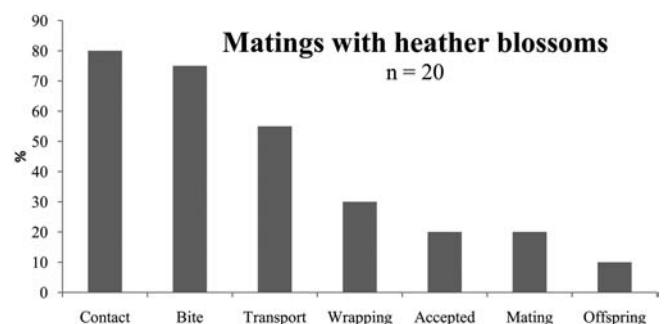


Fig. 13: Mating of *Pisaura mirabilis* with wrapped substitute heather blossoms ($n=20$ experiments, observation time: 30 min or until end of mating, 14 males, adult age 6-38 days/13 females, adult age 1.5-15.5 days). For further details see text.

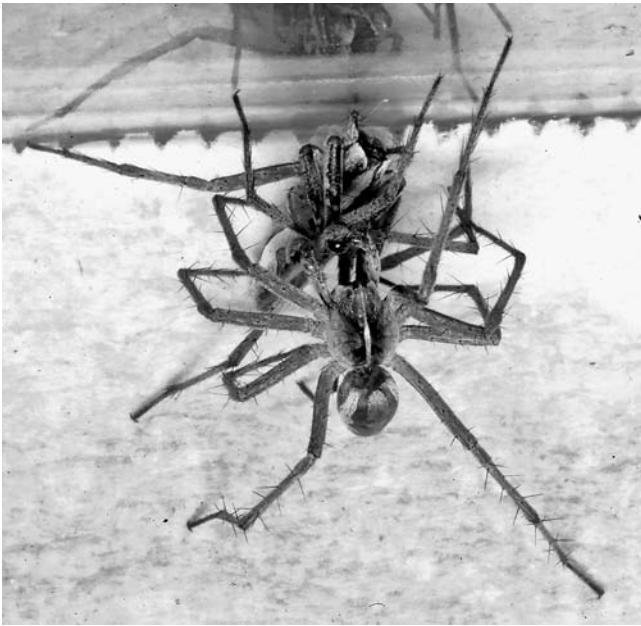


Fig. 14: Mating of *Pisaura mirabilis* without a gift. Male (below) is trying to lift the female with his bent legs (I–III left and II–IV right). She has just turned head up, and is now pressing down her body to the substrate with folded first leg pairs.

in reaction to these sudden movements of females. However, if the female remains still, the male tries to raise her with up to six legs (I–III left and right, but usually only of one side: I–II, II–III or I–III) in order to reach her epigyne (Fig. 14). Especially before insertions, but also while walking over the female, males attach draglines by discs to the substrate and different body parts of the females (substrate: 36.7%; female's chelicerae, prosoma, leg I: 46.7%; other legs and carapace: 16.6%; $n=30$). Males have problems orientating, because they may try to insert not only on the ventral side of the opisthosoma, but also on the prosoma or even on the female's head region. Once during insertion attempts a drop of fluid, probably sperm originating from the left palp, was sprayed onto the wall of the cage; insertions of the right palp had been successful just previously. Contrary to the normal procedure, males without gifts do not regularly change the inserting palps. In Fig. 15 the right palp is inserted, the female has raised her body, the male's legs III are incurved as in the normal case with a gift, but her chelicerae are near his left palp. During insertions the females' chelicerae are empty at first, but after a short time they make biting movements. At least some insertions ended when females tried to bite males (in leg III, the uninserted palp or the prosoma). Males react to these bites in two different ways: they may withdraw their extremities without terminating their insertions, or they may jump away, i.e. mating is terminated and the pair separate. I observed females chewing for a while on right leg III or the uninserted palp, until the male withdrew it. Insertions without gifts were very short, median only 18 s (further data in Table 4), significantly shorter than matings with different kinds of gifts ($p<0.05$ or $p<0.01$, K–S test). Nevertheless, two females produced spiderlings.

Females with prey, egg sacs or on nursery webs: Males *without* gifts bite the prey item (or gift) of the female and try to insert. However, unwrapped prey items or remains, or even a complete fly, often tear during separation of the sexes (compare similar cases above). Once a fly (*Lucilia*) was torn apart after been bitten by the male, with the result that the female fed on the head while he offered the rest to her; then she felt for him and laid her palps on this larger fly part. He withdrew his chelicerae from the fly, grasping it with his third legs, and inserted, while she was still feeding (first on the head, then the body of the fly). After they separated the female kept the larger part of the fly, while the male had the smaller part. In another case the male bit the fly remains of the feeding female. She ran away and carried him hanging onto the fly with her. Later he tried to catch a fly, unsuccessfully, and he went back to her, bit the fly remains again and inserted for a short time. During separation the fly tore apart, and the male released it from his chelicerae, added a disc with his spinnerets, grasped the prey of the female and inserted one palp, while his chelicerae remained in her prey. Then both fed together on her prey, and at the end the larger part remained with her, the smaller part with him.

When males *with* gifts encounter females *with* prey they usually offer their gifts or may wrap them again. Sometimes the male may even let his gift out of his chelicerae, still holding it with his third legs, and try to insert. I observed one female feeding on her fly while contacting his gift with her tarsi I and II; while he was inserting, she fed first on her own prey then discarded it and changed to the gift. Another female kept her prey



Fig. 15: Mating of *Pisaura mirabilis* without a gift. Note the swollen haematodochae of the inserted right palp (right arrow) and the position of the left palp near the female's fangs. The male's third legs, normally in contact with the gift, are incurved as is usual when a gift is present (left arrow), and his fangs are opening and closing with the changes in haemolymph pressure.

remains in her mouth, bit the gift and fed on both; during separation the male got a small part of the fly. Occasionally females may drop their prey items before grasping the gifts.

If a male with a gift encounters a female with an *egg sac*, he offers the gift. The female usually does not react or moves away. However, I observed a few cases of positive female reactions: one female laid her second egg sac aside and bit his gift, but several times she released it as soon as he began to jerk. In a second experiment two days later she behaved in the same way, but the male grasped her egg sac as well as his gift and spun both together; again the female first bit the six-day-old gift (fly remains) and then discarded it. In another case a giftless male, having met a female with her second egg sac sitting in her bell-shaped web, managed to insert his right palp three times for a short time, but this did not result in offspring.

Agonistic behaviour and behaviour of two males with one female (threesome)

What happens whenever two or more *P. mirabilis* males meet each other or when a second male encounters a mating pair? At first I thought that males would simply offer their gifts: she would choose one mate (or his gift), and the other male would continue to offer his gift. Sometimes this happens (Fig. 21), but males are rivals, and can show agonistic behaviour. For example, I observed one male jumping on a sexually excited rival and both forming catching baskets in the planted terrarium from which a female had just been removed. After separating both males retained their gifts, but in the evening of the next day one of them carried a double gift in his chelicerae (each part $3 \times 2 \times 2$ mm, loosely spun together), and the rival had no gift. After this I recorded lost gifts four times (hanging on a thread at a distance from a male or lying on the ground), and once, the larger male without a gift picked up a lost gift when near the female. I also observed another double gift and a struggle for it. Several times I saw males encounter each other, one or both with a gift, and simply jumping apart. However, I also observed one possibly sexual interaction between these two males with gifts: after contact with their front legs both jerked in a sexually excited manner, then they separated peacefully.

Male one	Male two	<i>n</i>	<i>nE</i>
- gift	- gift	2	2
- gift	+gift	17	16
+gift	+gift	17	15
+gift	+fly	11	8
+fly	+fly	4	3
Total		51	44 (86%)

Table 3: Number of mating experiments with one *Pisaura mirabilis* female without prey and two males with or without nuptial gifts in an artificial habitat (Fig. 2). - gift=male without gift, +gift=male with wrapped fly (remains), +fly=male with freshly caught unwrapped fly *Lucilia* sp., *n*=number of experiments, *nE*=number of experiments with male encounters.

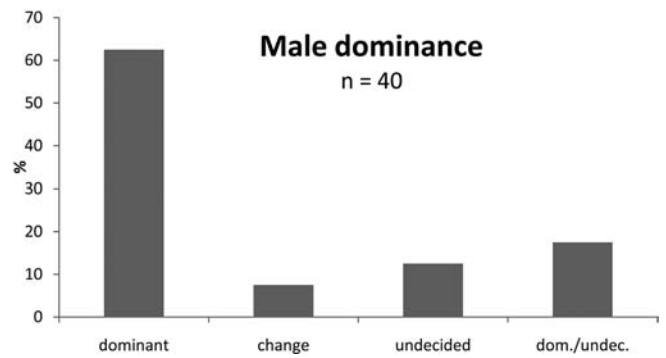


Fig. 16: Dominance of *Pisaura mirabilis* males. Dominant=male holds the fort, chases his rival away, or steals his gift (*n*=number of experiments with up to 16 encounters, dom./undec.=change between dominant and undecided).

Males did not encounter each other in all laboratory experiments because of the spacious terrarium (Fig. 2), but in 86% they did so once or several times (Table 3). They behaved agonistically in 40 experiments (Fig. 16), out of 44 with male encounters, and the second male interacted with the mating pair in 15 experiments. The following behavioural patterns were observed: (1) *Flight and chase away*: If two males encountered each other, one male fled to some extent to the ground or hid for several minutes under loose blotting paper, whereas the other one first stopped walking with raised first legs, then walked on with jerky steps. In other cases both males ran away in different directions. Males which had fled once did the same again, even before they came into contact with the approaching rival. (2) *Disturbance of gift-production*: When a male approached or came into contact with a prey-wrapping rival, the latter usually grasped his gift with his chelicerae and chased the rival away, or both grappled with each other. However, I also observed a male continuing wrapping after leg contact with a rival, which fled. In another case, the male left his gift attached to the substrate, chased his rival, then returned and searched for the gift which meanwhile had been seized by the female. (3) *Prey capture behaviour*: The female usually behaved peacefully; only once was a non-excited fleeing male almost caught by her. Males without and with gifts clasped each other with all legs incurved as typical for prey capture, then fell to the ground, where they separated. Sometimes they bit the legs of rivals; after separation the situation was either the same as before, or sometimes a male, even one with gift, had stolen the rival's gift. No male was captured by a rival or by a female or vice versa.

In nearly two-thirds of all encounters one male was dominant every time (and in 93.5% usually the winner); only seldom did the dominance change or were encounters undecided (Fig. 16). There were no differences between males with gifts versus males without gifts, or younger versus older ones. Larger males usually won fights for gifts and chased smaller rivals ($n=32$, $n+ = 23 = 71.9\%$, $\chi^2 = 6.125$, $p < 0.02$).

In 15.8% of all recorded encounters ($n=158$) between males with and without gifts they clasped each other, i.e. formed catching baskets. In most cases the possession of the gift remained unchanged, but at the end of the

Gift type	Insertion* (min:s)	NIns.	Copulation* (min:s)	Mating* (min:s)	Female	Winner (%)			Offspring (%)
						Male	Both	Lost	
G (L)	6:11 ± 11:07 (0:02–58:26) (311)	3.9 ± 4.5 (1–30) (53)	29:56 ± 26:25 (0:05–122:16) (65)	37:53 ± 25:26 (1:15–126:39) (56)	59.6 (57)	40.4	0	0	38.1/47.1 (42)
L+	8:57 ± 13:42 (0:02–50:54) (142)	4.1 ± 4.1 (1–16) (24)	39:45 ± 35:43 (0:04–141:33) (32)	68:58 ± 57:59 (13:55–148:54) (13)	74.3 (35)	22.9	2.9	0	61.5/80 (13)
L –	10:44 ± 14:10 (0:02–49:12) (27)	2.6 ± 1.6 (1–6) (10)	26:20 ± 26:22 (0:02–75:55) (11)	30:11 ± 33:04 (3:42–83:58) (8)	59.1 (22)	0	40.9	0	14.3/20 (7)
D	5:33 ± 7:03 (0:01–26:34) (33)	3.3 ± 3.1 (1–11) (9)	18:17 ± 11:47 (0:08–37:19) (10)	18:11 ± 9:37 (4:03–38:47) (10)	72.7 (11)	18.2	0	9.1	7.1/12.5 (14)
HB	6:57 ± 5:21 (0:02–17:05) (9)	3.3 ± 3.2 (1–7) (3)	15:38 ± 14:06 (7:18–36:40) (4)	23:44 ± 21:40 (8:53–55:11) (4)	50 (4)	25	0	25	18.2/50 (11)
– G	0:41 ± 0:57 (0:01–04:09) (30)	2.7 ± 1.7 (1–6) (11)	1:53 ± 2:38 (0:01–9:04) (10)	– –	– –	–	–	–	12.5/28.6 (16)

Table 4: Comparison of *Pisaura mirabilis* matings with different gifts. G(L)=wrapped fly remains of *Lucilia* sp., L+=wrapped *Lucilia* sp., L – =unwrapped *Lucilia* sp., D=wrapped *Drosophila* sp., HB=wrapped heather blossom, – G=without gift; Offspring=percentage of matings producing spiderlings in all experiments / % in experiments with insertions, number of experiments in brackets; *=time data reported as means ± SD, min:s with range and n in brackets; NIns.=number of insertions per mating.

experiments nearly one-third of the gifts were stolen by the rival, and two gifts were lost (Fig. 17).

Gift robbery strategy: I recorded four different results of male–male encounters: (1) Bitten rival lost his gift: a giftless male jumped at a rival with gift, they clutched each other, then the latter fled, settled down and groomed his slightly bent right leg II for a long time, whereas the winner seized the gift, walked away with jerky steps and wrapped it. (2) Food for the sexually exhausted rival: at the end of mating the gift remained with the female, and the male spun a sperm web. The second male with gift jumped at the recently mated rival. After separating from their catching baskets the situation had changed: the second male fled and searched for his gift, while the winner fed on the stolen gift. (3) Won and lost or lost and regained: two gift-carrying males grasped each other. After separation, one was searching for his gift, while the other first held both gifts with his bent legs, then lost the stolen one while walking, whereupon the loser felt it and regained it. (4) Double gifts obtained by robbery: two males with gifts clutched each other. After separation one male kept his gift, grasped the second gift lying nearby on the ground, and added it to his own by spinning, thus forming a double

gift. In an encounter between two other gift-carrying males, one lost his gift and searched for it, while his rival, walking excitedly with jerky steps, picked it up. A few moments later the female bit the gift, but only half of the double gift, which had not been wrapped together by the dominant male. He then presented his gift below her without trying to insert.

What happens when two males without gifts encounter each other in the presence of a female? I observed once a male hunting his rival and even trying to catch him. Then the dominant male stole a dry dead fly which had been taken by the rival just before, and later he

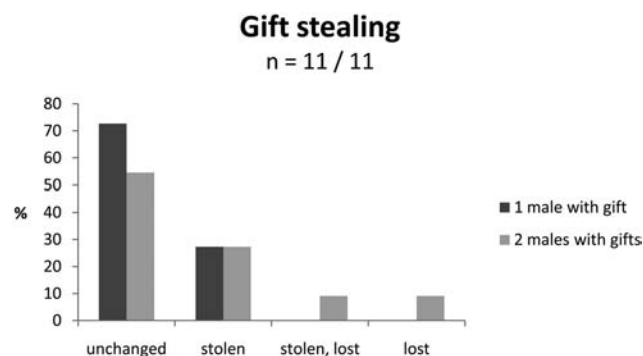


Fig. 17: Gift stealing by clutching each other with catching baskets of two marked *Pisaura mirabilis* males in presence of a female (n=observed cases of clutching; unchanged=incl. gift loss for a short period; stolen, lost=gift stolen for a short period, then lost).



Fig. 18: A marked male of *Pisaura mirabilis* (with three yellow spots on the back of his opisthosoma) is wrapping his own and a stolen gift (fly, *Lucilia* sp.) together, thus producing a giant double gift.

stole a freshly caught fly from his weaker rival and wrapped both flies, thus producing a giant double gift (Fig. 18).

Thus, males have evolved a strategy named “gift robbery”. They may win a gift without using time and energy by lurking for and catching prey (but need a little energy for the struggle for the gift), and save some silk material for wrapping it, if the stolen gift is still wrapped. Even if a male already carries his own gift, by robbery he enlarges it and produces a double gift by wrapping both together. If this wrapping together is omitted, one part may be lost during the search for a female or she may bite only one part and he has to wait offering the other half.

Peaceful and sexual male–male encounters: Under semi-natural conditions, I once observed two males lying on the ground and biting one gift. Then one of them, jerking in the typical manner before an insertion attempt, released his chelicerae from the gift, but did not try to insert. A few minutes later the larger male offered the stolen gift to a female, and the smaller male, having caught a cricket, produced a new gift. Afterwards both males alternated in offering their gifts to the female. During the night, the males again bit one gift, the male below jerked and tried to insert, whereupon both fell down to the ground and separated. One hour later at 23.00 h both males again offered their gifts to each other near the female.

In the artificial habitat, two old males with gifts (adult age 68 days=83.4% relative age, and 58.5 days=84.8% respectively), after feeling each other for several minutes with their front legs, slowly separated. In this experiment the female, having discarded her first egg sac, often released the gift with the result that one or both males fell to the ground. Several times both males tried to copulate with each other. Once one male dropped his gift, seized his rival's gift, and then tried to insert (Fig. 19).

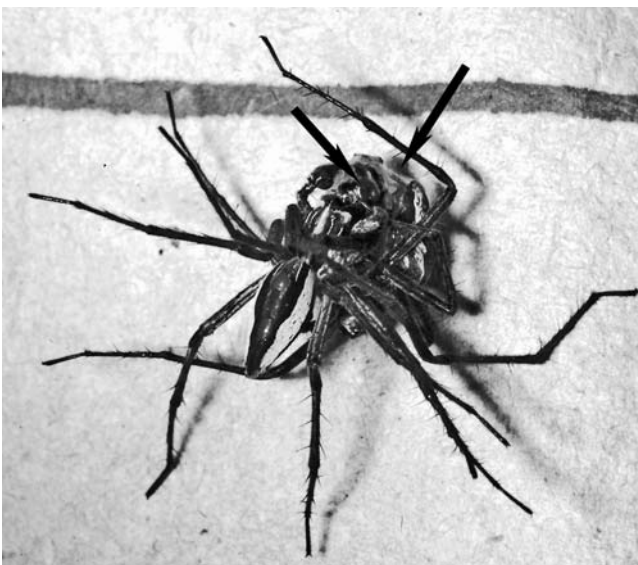


Fig. 19: Two males of *Pisaura mirabilis* with one gift (left arrow). The head downwards-sitting right male is trying to insert his right palp on the underside of his head up-sitting rival. Note his security thread attached to the gift (right arrow).

Disturbance of mating: Under semi-natural conditions, the mating pair were disturbed during different phases (pair in leg contact, both biting the gift, or during insertion) by a second male, by crickets and once by the light beam of the observer, i.e. by intraspecific, interspecific and non-biological causes. Three different situations between rivals were recorded: (1) Male with gift chases giftless rival and mates. Once while a female and a giftless male were feeling each other, a second male with gift jumped at his rival and chased him away. Then he offered his gift to the female for three hours, until she accepted and the first insertion began. (2) Giftless male guards the female. Once in the evening a male wrapped his gift near the female; some minutes later a larger male without gift clutched his rival, chased him away, walked excitedly with jerky steps back to the female and again chased away the returning rival which then hid in a corner. Thus, the larger male seemed to guard the female. Afterwards the giftless male lurked for prey on the ground (with widespread legs), where crickets were moving, then he walked back to the female and made leg contact. Later a second clutching of the males was observed. (3) Intervention causes only interruption. Several times a second male touching the mating pair caused the female to jerk back and end the insertion, but the first male hanging on the gift remained in contact with her, and the second male jumped away. A few minutes later the insertion of the same palp was resumed. In other cases the second male (with or without gift) clutched the mating pair, resulting in separation but unchanged possession of the gifts. Once a female, having just bitten the gift, lost contact with her mate after a second giftless male had contacted the pair. Both males clutched each other for a short time, and the first one kept his gift, while the second fled. The female walked away, turned and climbed on her dragline back to her partner. One hour later mating occurred, and at the end the female kept the gift. In some cases the second male did not disturb the mating pair immediately, e.g. once at night a larger male offered his gift near the mating pair and, while in contact with a leg of the inserting male he rubbed his legs, but the insertion continued. Twenty minutes later all three were found separated: the small male with gift, the female and large male without gift.

Rival encountering mating pair: In the artificial habitat, mating took place in 55% of all experiments ($n=51$). However, because of the frequent dominance of one male (Fig. 16), only one male was successful in 93% of these 28 matings, whereas on two occasions both males inserted alternately with the female (Fig. 20). In 15 experiments the second male came in contact with the mating pair up to eight times. In some cases the single male passed close to the pair without showing any reaction. Contacts were made accidentally during normal or jerky walking, by following female draglines, or by locating the heavy jerks of the rival male preceding the release of the gift at the beginning of an insertion. In 14 out of 15 experiments the first contact of the second male with the pair was a simple leg contact, only once did he jump at the pair, causing them to separate. Nearly

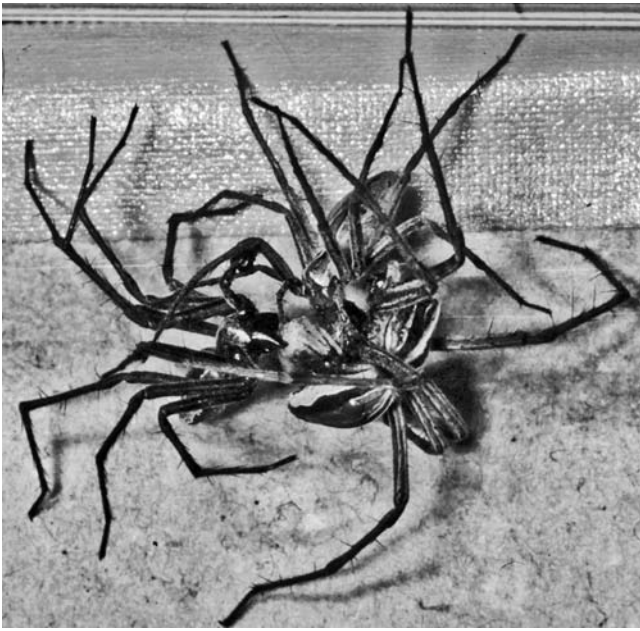


Fig. 20: Threesome: female (above) and two males of *Pisaura mirabilis* grasping one gift. The right-hand male has climbed up to her left side and is trying to insert his left palp, while the other male and the female are biting the wrapped fly (*Lucilia* sp.).

two-thirds of all encounters ($n=45$) were leg contacts, followed by jumps on the pair (20%), the remainder being various behaviours such as grasping the gift of the pair, insertion attempts on the other male and running towards the pair. After leg contact the second male usually remained motionless for some time with his first leg pair raised, and then he felt for the pair or ran below them and offered his gift nearby (Fig. 21). Giftless single males turned around and lurked for prey, jumped on the pair forming clusters of all three pisaurids or both males, or seized the gift of the mating pair. In 53% of these disturbances ($n=45$) by a second male the first male was just inserting ($n=19$) or attempting to insert ($n=5$), the remaining pairs ($n=21$) were holding the gift. In half of these 24 mating disturbances the second male caused the end of the insertion attempt, and in half of these even the separation of the pair. However, there were also real threesomes, i.e. two males and one female with one gift being bitten (example 5, see below); in (5b) both males succeeded in inserting, but only for a short time (1:24, 2:28 min: s) without producing offspring.

The female's perspective: The female reacted to leg contact of a second male in different ways: (1) no reaction, i.e. she continued feeding on the gift; (2) she beat with her legs against the new male; (3) she jumped in prey capture mode against him; (4) she ran away, i.e. ended the insertion and the pair separated or her mate, hanging on the gift, was carried away by her.

Chances for a giftless male: All possibilities for a giftless male to mate with a female are summarised in Fig. 23: without a gift, with a wrapped surrogate or with a self-produced or stolen gift.

Observed variations when a second male contacts a mating pair: (1) *No disturbance of the pair:* Male 2, having lost his gift in a struggle with his rival, walked with jerky steps and twice touched the copulating pair

with his front legs, then walked away and settled down with all legs widespread, i.e. lurking for prey. (2) *Interruption by the rival:* Male 2 without gift, having come in leg contact with the copulating pair, jumped at them; they fell down, the insertion was terminated, and male 1 kept his gift. Male 2 then jumped a second time at his rival, both formed catching baskets, but male 1 kept his gift again and maintained his ground, whereas his rival ran away, settled head down, groomed and tried to catch an added fly. (3) *Female's defence and transport of the mate:* Walking excitedly with jerky steps, the second male touched the mating pair; the female reacted with leg beating, causing rapid flight of the second male to the ground and termination of the insertion of male 1, but he bit the gift and was carried away by her (see Fig. 8). Then male 1, having typically jerked and moved to the female's left side inserted his left palp, while the second male ran upwards towards the pair, stopped at a distance of 2 cm, then walked closer and closer with his first leg pair raised. The female jumped towards him in typical prey capture manner, with the result that male 2 fled and male 1 bit the gift and hung on it while again being carried away by her. (4) *Gift offering and approach of the second male:* Male 2 walked with jerky steps towards the pair and after a short leg contact he offered his gift; male 1 finished an insertion, bit his gift and sucked on it while the female was still feeding. Male 2 then rubbed his legs and approached; the jerking of male 1 before a new insertion attempt caused the approach of male 2, which resulted in total separation of all three spiders; the female won the gift, male 1 walked away, and male 2 continued offering his gift. (5) *Threesome of two males and a female:* If the second male seizes the gift of the mating pair, we have a situation where two males and one female grasp one gift: (5a) *Male 2 without gift made leg contact with the mating pair:* After 25 s the first male terminated his insertion and bit the gift again; male 2 bit the gift of the pair, i.e. all three were now biting one gift. Jerking by male 1 caused his rival to walk away; coming back, the latter seized the gift again; however, the female dropped the gift and both males continued

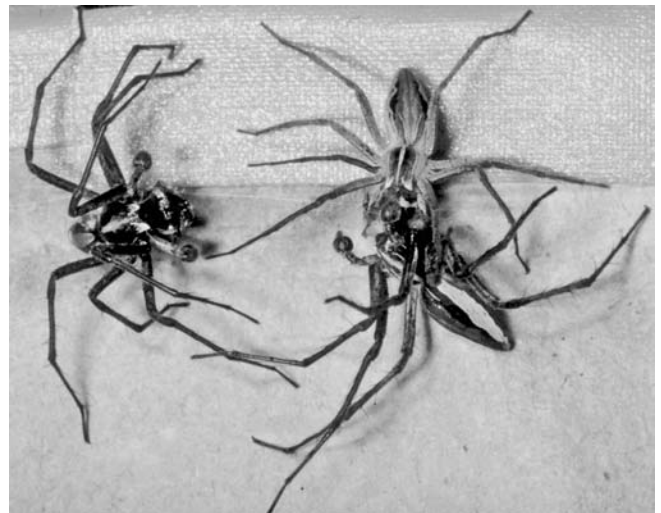


Fig. 21: A second male of *Pisaura mirabilis* presenting his gift beside a motionless resting pair (female above).

biting it. Finally, male 1, having shaken off his rival, won his gift back. (5b) *Discarding own gift and biting that of the couple*: The female and male 1 were biting the gift; the second male also offered his gift. The female released her fangs as soon as the male started to jerk. Twenty minutes later male 1 walked away, whereas male 2 took his rival's place. The female felt for and bit the gift of male 2 and walked a few steps back/up, thus carrying him hanging on the gift. Male 1 offered his gift beside the pair (Fig. 21). Two minutes later male 1, having discarded his gift from his fangs (first it hung under him, and then fell to the ground), tried to insert his left palp on his rival, which together with the female was still biting his gift. Male 1 then seized the gift of the pair, thus two males and one female were now holding one gift (Fig. 20). Male 1 inserted his left palp for 84 s and bit the gift again. Male 2 inserted his right palp three times for only a few seconds and returned to the gift as soon as male 1 started jerking. Male 1 jerked, released his gift, climbed around the gift and over his rival, causing all three to fall to the ground and separate. The female walked away, leaving both male rivals biting the gift. Then male 1 walked upwards with his rival hanging on the gift, followed by the reverse: male 2 walked with gift and rival, then he stopped, withdrew his chelicerae from the gift and fixed it by wrapping it to the ground. After grooming a leg, he tore the gift off, showing excitement by leg rubbing and walking with jerky steps, while his rival was still hanging on the gift (Fig. 22).



Fig. 22: Male of *Pisaura mirabilis* carrying his rival hanging on the gift in the same way as females carry males (see Fig. 8). Note the outstretched legs and the raised palps of the hanging male. Seven minutes previously, both males and a female simultaneously were biting one gift (similar situation as Fig. 20), then they fell down and separated; the female ran away, and one male climbed up the pieces of wood in the centre of the terrarium (see left and right under his tarsi), stopped, fixed the gift and groomed; then he continued carrying the gift with the other male still hanging on it.

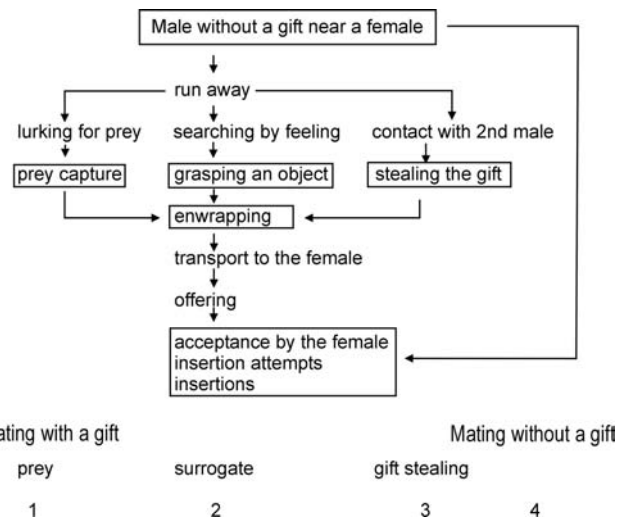


Fig. 23: Four ways for a giftless *Pisaura mirabilis* male to mate with a female.

Sixteen minutes later the female grasped the gift again, and male 1 tried to insert on the right side of his rival, resulting in the release of the gift by the female. Now both males bit the gift again, and male 1 tried to insert his right palp on his rival (Fig. 19). One jerking of the latter caused male 1 to bite the gift again; male 2 carried the gift with his rival hanging on it, to the female. She seized it several times, but released it at once as soon as the male started to jerk, thus causing the males to fall. The males again tried to insert in each other. Then male 1 ran away, leaving the gift and grooming rival behind him. The female grasped the gift again, and short insertions followed. Then male 1, walking jerkily, touched the female while his rival was inserting, resulting in his rival biting the gift at once and being carried away by her. Now male 1 bit the gift again, resulting in a new threesome. Short insertions by male 2 followed, but were ended by jerks from male 1, who then tried to insert on his rival. Finally, the female released the gift and walked away, both males bit it and separated, when the second male kept his gift and wrapped it (for more details of 5b with real-time data see Nitzsche, 1987: 164–166, protocol 6; relative age of the female nearly 49% after discarding first egg sac, males between 83 and 84%).

Intersexual aggression and cannibalism

As described above, in the planted terrarium a large female killed a smaller one, but no male was caught by a female. The same was true for a male and female living together for seven days in the keeping box (Fig. 1); however, on day 5 she was observed feeding on his autotomised left leg II; I recorded two copulations before this and four afterwards, then they were separated because she had produced an egg sac. Females tried to catch males in 7.7% of all mating experiments with different kinds of gifts ($n=168$, data in Nitzsche, 1987). They attacked both unexcited and excited males of different ages, with or without gifts, and a male while wrapping his gift. In addition to these 13 cases of

aggression, two females feeding on flies tried to catch unexcited males. One discarded her fly and first bit the male (right leg II) and then his unwrapped fly. The other female kept her fly, and the giftless male escaped. Thirteen capture attempts occurred before the acceptance of a gift, one after acceptance but before an insertion, and one after insertion ($n=15$). However, females often interrupted the full catching procedure: they stopped after a short jump or at the moment of the first contact with the male. Usually the males escaped. Sometimes an attacking female bit the gift, which had been rapidly turned by him in her direction, instead of the male, and mated. Males were bitten exclusively in their front legs (left I, left II, right II); two died, and three escaped, twice because the females changed their bite from male to gift, and once because the heavily jerking male freed his leg from her chewing chelicerae.

In only 1.8% of all mating experiments *with and without* gifts ($n=222$, Nitzsche, 1981, 1987, data summarised) were males killed by females. The four cases were as follows: (1) the female pursued the male and caught him after the addition of a fly, but two days later she copulated with another male; (2) the male wrapped a fly in the presence of an already mated female, which suddenly caught him; (3) an unexcited male was caught by the female and bitten in left leg I, and the small *Drosophila* gift was lost; (4) the female first accepted the small fruit fly gift and short insertions, and then suddenly clutched him (Fig. 9). Note that in other cases with similar age, nourishment and mating conditions, males were not caught.

During all laboratory experiments not only females but even three males without gifts pursued females; however, despite forming catching baskets, they did not bite them. Probably these males were simply searching for prey to produce gifts. Note that an old male may even be caught and wrapped as a gift by a younger rival (not in the experiments described here, for photo see Nitzsche, 1981: 147).

Discussion

1. Perception and recognition — not a shred of a sensory trap

How does the female of *P. mirabilis* recognise a male and vice versa? I did not examine the senses involved in courtship and mating, but I think that a statement such as “Vision is vital for hunting spiders because they use motion, shape and size as cues in prey catching and courtship” (Stålhandske, 2002) is not the best basis for a theory about “sensory traps”. Of course, to human eyes there is a high degree of contrast between a densely wrapped white gift and the often dark body of the male (which enables faster warming up and longer activity at night?). However, not all males are dark, not all gifts are white, and many of them are very small (Nitzsche, 1988). In the field the optimal lighting of the laboratory is not present, especially in the evening and on moonless and starless nights within the herbaceous stratum between

stems of grass. Homann (1931) observed no reactions to resting flies, but capture attempts for all moving things such as flies, dummies, even shadows outside the cage. He concluded that the eyes are only capable of perceiving movements, but not of identifying forms (see also prey capture analyses in Nitzsche, 1981). Within the last decades the senses of other pisaurid species have been examined. Williams (1979) observed a New Zealand *Dolomedes* species catching prey in complete darkness; even blinded individuals caught flies in flight. Bleckmann & Barth (1984), examining the senses involved in prey capture on the water surface by *Dolomedes* species, found that even blinded and trichobothria-shaved individuals turn and run towards a wave source (normally a fidgeting insect), though not as rapidly or as far as intact spiders. In addition, Barth (2001) mentioned that the night-active *Cupiennius* (Ctenidae) may be able to see in the moonlight at night but cannot recognise a potential sex partner. It may be similar in *P. mirabilis*, citing Bristowe & Locket (1926: 331): “In *Pisaura* sight does not appear to be so well developed, and the male possesses no epigamic characters, so the attid and lycosid kind of courtship would not be suitable.” Moreover, many pisaurids are web spiders; probably all members of the family were originally web-builders and many species have retained the web for their whole life, whereas in other cases only the early instars build webs. Thus, the early instars of the European species build small “hunting-webs” (*P. mirabilis*: Berland, 1927; Lenler-Eriksen, 1969; Homann, 1971; Nitzsche, 1981; *Dolomedes fimbriatus*: Nitzsche, 2007, 2008).

The absence of enlarged anterior median eyes, the building of webs as juveniles, and the typical “clubionid-like” (Nitzsche, 1981: 130) feeling behaviour preceding the biting of the gift, suggest that females of *P. mirabilis* are unable to recognise males or gifts by eyesight. This seems true also for males searching for lost gifts and prey by feeling with their forelegs (this paper). Males behave in the same way as females do when searching for lost egg sacs (e.g. Schmidt, 1955). A female may recognise a walking male by her trichobothria and slit sense organs and his movements also by eyesight, but the position of a gift-offering male only by perception of his jerking body and especially his typical leg rubbing via the substrate and air vibrations (however, the rubbing of legs are fast movements and may also be perceived by eyesight). Males of *P. mirabilis* probably identify conspecific females first by contact sex pheromones on their draglines and the substrate (Bristowe & Locket, 1926: 330; Nitzsche, 1981: 123–127) and then by touch. Gaskett (2007) gives an overview of the current knowledge of pheromones in spiders, also citing papers with observations and experiments on sexual pheromones in other pisaurids (*Dolomedes* species). Thus, it seems unlikely that there is any optical identification of the gift by the *Pisaura* female as Stålhandske (2002) suggests for her hypothesis “nuptial gifts as sensory traps for females”; this had already been considered and rejected by Van Hasselt (1884). My observations (this paper) indicate that the European

nursery-web spider is not capable of identifying shapes; as shown by, e.g. males passing near motionless females, offering their gifts to mating couples, and searching by walking and feeling in circles. However, at very close range, visual identification of the gift and the degree of white colour may be suggested by the female's behaviour at the moment when she stretches out her palps after having felt the male and orientated to his centre. Then she obtains chemotactile information from the male silk around the prey; thus, the flavour of the gift's silken cover and/or of the prey may be more important than visual stimuli. Furthermore, it is likely that a *P. mirabilis* female is able to discriminate between the silken cover of her egg sac and of a gift, because even salticid females of the genus *Portia* with good eyesight are able to do this (Clark & Jackson in Huber, 2005: 367). If there is a special sexually appealing substance on male silk, it may be why males eagerly wrap white gifts with additional silk in the presence of unwilling females (Nitzsche, 1987: 53–58; Lang, 1996). Or perhaps this male behaviour is only an expression of excitement or a displacement activity without any benefit? Additional wrapping of gifts beside reluctant females also occurs in trechaleid males with nuptial gifts (Lapinski & Tschapka, 2009). Concerning their mating and cocooning behaviour, these spiders are intermediate between *P. mirabilis* and lycosids: courtship and mating occur with a gift, but the male mounts the female, and the flat egg sac is fixed to the spinnerets (Costa-Schmidt *et al.*, 2008), i.e. there is no similarity of nuptial gift and egg sac; that suggests there is no “sensory trap” (see also the experiments of Bilde *et al.*, 2007).

2. Special mating features

As in all spiders, *P. mirabilis* males look for and court females. However, contrary to most other species, here we find a prey-catching behaviour forming a basis for producing nuptial gifts. This also involves a searching behaviour for immobile or slow-moving animals or plants, an intensive wrapping of prey items, remains and substitutes, the carrying of the gifts grasped by the chelicerae for up to several days while searching for females, and the special offering position of the gift head upwards below the female accompanied by leg rubbing. Furthermore, males may struggle for the gifts of rivals and mate in special positions, first with raised palps, then with heavy jerking and shaking the female before moving to her underside, accompanied by the ability to bite the gift immediately if the female should move, and to let themselves be dragged off by the female so as not to lose contact with her and continue mating.

Females have developed fewer adaptations for mating with gifts: a “clubionid-like” walking and feeling associated with biting the gift, which is totally different from the normal prey-catching behaviour, the raising of the legs in answer to the heavy jerks of the male, and a sideward movement additional to the normal catching basket for winning the gift.

Prey and gift searching, post-immobilisation wrapping of prey and gift transport

Unlike the immature stages, which lurk for prey within their webs, and even in contrast to penultimate males and adult females, excitedly walking *P. mirabilis* males search for lost gifts, prey remains and objects suitable for a gift nucleus (Nitzsche, 1988; this paper). This behaviour corresponds to that of females after having their egg sacs removed. The same genes may control this behaviour in both sexes. By having both behaviours, the normal sit-and-wait and the searching strategy, males achieve a wider prey spectrum than females and immature stages (Nitzsche, 1988).

Males, females, penultimate and immature stages all wrap relatively large or multiple prey after killing it with poisonous bites (“post-immobilisation wrapping of prey”, Rovner & Knost, 1974), and fix it in position while performing grooming activities, locomotion or drinking, and feed on it later (Nitzsche, 1981, 1987, 1988). Sexually isolated males produce densely wrapped prey items (gifts) (Leighton, 1969), whereas males of the trechaleid *Paratrechalea ornata* (Mello-Leitão, 1943) produce gifts only after contact with female silk or females themselves (Albo *et al.*, 2009).

Leg rubbing

“Tarsal rubbing” is an indication of sexual excitement in trechaleid males (Costa-Schmidt *et al.*, 2008), also known from many other spiders, e.g. Lycosidae (Bristowe & Locket, 1926) and Araneidae (Robinson & Robinson, 1980). For *P. mirabilis* the term “leg rubbing” is more accurate, because males rub their tarsi, metatarsi and tibiae. The rubbing causes air- and substrate vibrations, which seem to identify the male as a sexual partner, because the female sometimes reacts by turning directly to the male or by interrupting prey capture (Nitzsche, 1987). Leg rubbing also exists in earlier instars and females of *P. mirabilis* in the context of cleaning mouthparts after feeding (Nitzsche, 1987: 104–109). Thus, it is suggested that sexual leg rubbing originated in a cleaning function, e.g. from clearing away female silk, and became ritualised as a signal function, now established as a fixed part of courtship. The male discloses his identity by “leg rubbing”, which functions well on plants within the herbaceous layer, but also on silken threads and webs, which the ancestors of *P. mirabilis* may have inhabited. It is unknown whether special stridulatory structures or glands secreting pheromones in the male's legs may also be involved.

Raised palps

Why do *P. mirabilis* males raise their palps when the pair are biting the gift together (Fig. 5), not as shown by Bristowe (1958: plate 20)? This raising of the palps seems to be arduous, because the palps slowly sink down and are lifted again. Perhaps this movement is a signal to her, or perhaps there is a sensory function, e.g. perhaps the trichobothria on the tips and the ventral side of his

palps perceive any small movement of the female. Or maybe there are glands on the ventral side of the male palps emitting a volatile pheromone to calm her, when the air moves up to her sitting head downwards above him within the herbaceous layer?

Thanatosis

Bilde *et al.* (2006) published a paper with the sensational title “Death feigning in the face of sexual cannibalism”. This male behaviour was thought to have evolved “under the risk of being victimised by females”. Experiments were done in terraria which did not allow the spiders to climb up, perhaps a reason for the high rates of this so-called “feigning death” behaviour that were recorded. Results with few attacks obtained in previous studies by other authors were labelled as “artefacts” of “well fed” spiders. However, well fed females do not accept gifts (Le Pape, 1974). Hansen *et al.* (2008) retained the key word “thanatosis”, but suggested that this male behaviour “functions as an adaptive male mating strategy to overcome female resistance”. That is probably correct, but the terms “feigning death” and “thanatosis” for this special posture of *P. mirabilis* males during mating also need changing, and a new term such as “dragging off” should be substituted, because a dead spider looks quite different: its legs are bent, caused by loss of blood pressure (for photos see Nitzsche, 2007: 58). During the so-called “death feigning” the male remains motionless, but his legs are outstretched and his palps raised (this paper) — for which high blood pressure (legs) and muscular energy (palps) are needed. Moreover, Jones (1995) described a totally different posture as “feigning death” in *P. mirabilis*. In the field he observed a single specimen changing several times from a “crumbled appearance of a shed skin” with its limbs “loosely and irregularly curled under its body” (the feigning death position) to a position with its first two pairs of legs outstretched. He interpreted this behaviour as a response to danger (by photographing the spider with flash), typical for thanatosis. The so-called “feigning death” of Bilde *et al.* (2006) does not function against aggressive females but is simply an adaptation, an evolutionarily stabilised trick of the male, in cases of disturbance during insertion not to lose contact with the female within the dense three-dimensional habitat. This behaviour enables males to increase the number of insertions, because males simply grasp the gift and let themselves be dragged off when females run away. Females may run away in order to retain the gift, but also when disturbed by enemies, other males or even potential prey (this paper). Therefore, in my theses and my books (Nitzsche, 1981: 131; 1987: 152–154; 1999: 128; 2007: 138) I called this behaviour simply “being transported by the female”, following a short description by Le Pape (1972: 23: “Le mâle se laisse trainer par la femelle”). It seems to be a kind of akinesia, comparable to the behaviour of lion cubs when mouth-transported by their mother. However, stretching legs and raising palps costs energy, so this behaviour is not as passive as it seems. The basis for this successful male

behaviour is his mating position, especially the position of his chelicerae near the gift during an insertion, his fast reaction to any movements of the female, and his holding the gift from four sides, i.e. by an attached dragline, the third pair of legs and the uninserted palp.

3. Mating with different kinds of gifts

Wrapped prey — the typical way

The typical way for a *P. mirabilis* male to mate and reproduce, known since 1884 and described by Van Hasselt as an anomaly, is mating with a nuptial gift produced by a male by capturing prey and wrapping it with silk, thus forming a ball or an ellipsoid. My observations described here show that *P. mirabilis* males produce by wrapping, in the laboratory and under semi-natural conditions, gifts of different sizes, forms (round and oblong) and quality, depending on prey size and shape (fly, cricket, leg of a cricket). They also collect prey remains (carion) and parts of plants (heather blossoms) and enlarge their gifts by adding further prey items or gifts stolen from rivals. Gifts may also increase in size by the accidental gluing of dead insects and plant parts onto the silken cover, but only for a moment unless wrapping follows, thus preventing them from getting lost. However, most gifts collected in the field were small and only a few large, e.g. a wrapped opilionid (Nitzsche, 1988: 358–360).

Freshly caught unwrapped prey

Pisaura mirabilis females accept both wrapped and unwrapped prey items as nuptial gifts (this paper). In the field, nearly 83% of the prey carried by males was wrapped (Nitzsche, 1988). The remaining prey items, e.g. a small cicada (Hemiptera: Cicadidae), were either eaten by the male or would be wrapped later. At the moment of prey capture, a hungry female sitting nearby may grasp the male’s prey, especially a whirring fly. In the laboratory, Bristowe & Locket (1926: 331) described this situation: “. . . the male did not have time to wrap up the fly, but the female leapt down to him and seized it from him.” Schmidt (1955: 566) also observed this, adding that a female discarded her own prey (or remains, as I observed?) before she bit his fly. I also observed these fast reactions of females (Nitzsche, 1981). Bilde *et al.* (2007) measured the presentation time, i.e. the time from offering until acceptance of the gift, and found that unwrapped (or loosely wrapped) freshly caught flies were accepted significantly more rapidly than wrapped ones (see also Andersen *et al.*, 2008). It is not clear whether the smell of insect blood elicits the female’s prey-catching behaviour, or whether the silken cover of a densely wrapped fly masks the prey odour. Possibly the silk of the gift emits a volatile pheromone that induces sexual arousal in the female. Note the difference between a fast prey capture and the biting of a moving freshly caught fly compared with the slower feeling approach by the female to the offering male.

Males with unwrapped flies may be killed more often than males with wrapped flies (Andersen *et al.*, 2008; Hansen *et al.*, 2008). Moreover, an unwrapped prey, especially a fly, and its frequent breaking into two parts (this paper), may cause problems for the male to find the female's epigyne. The duration of insertions, copulations and matings does not differ between unwrapped and wrapped flies used as gifts (Nitzsche, 1987: 135–146; Bilde *et al.*, 2007). However, the female usually wins the gift (Nitzsche, 1981: 139; 1987: 155; this paper). Andersen *et al.* (2008) found that unwrapped flies were stolen (accepted without copulation) by females more often than were wrapped ones, a hint for a possible motivation function of gift silk: guiding the female away from foraging to mating mood.

Wrapped prey remains, blossoms and egg sacs

Nuptial gifts collected in the field contained both complete prey items and prey remains (Lécaillon, 1905; Gerhardt, 1924; Nielsen, 1932; Pénicaut, 1979; Nitzsche, 1987; summarised and discussed by Nitzsche, 1988). Moreover, Schmidt (1955: 563) also found wrapped heather blossoms in the field. Mating with such wrapped prey substitutes is possible (this paper). The plant content of this kind of gift is not edible, but the silken envelope enables the female to grasp the gift in her chelicerae, and perhaps the male silk may identify it as a nuptial gift (this paper, for photos see Nitzsche, 1987: 132). In the laboratory, not only prey remains (e.g. Bristowe & Lockett, 1926: 331; Thomas, 1928) and heather blossoms and stems (Schmidt, 1952, 1955; Nitzsche, 1987), but also other objects were wrapped and used as nuptial gifts (Spassky, 1935: small chip, piece of twig; Nitzsche, 1981: foam material). Egg sacs can also function as gifts and were eaten by females which had not produced one (Bilde *et al.*, 2007), whereas a female whose egg sac had just been removed did not accept the gift of a male, but bit him and drove him away (Schmidt, 1955).

There are striking parallel behaviours in the autumn spider *Metellina segmentata* (Clerck, 1757) (*Meta segmentata* in older literature). In this species the male does not start his courtship until the female bites a prey item in her web (Prenter *et al.*, 1994a). Schmidt (1986) observed prey remains, a small leaf or a needle blown by the wind in the female web acting as triggers for the male courtship display. Males even wrapped scraps of paper and wool when females repelled them for longer.

Optimal gift

Gifts differ not only in size but also in age and quality. They can be more or less densely wrapped, and serve as food for males during several days of being carried (Nitzsche, 1988); ultimately, they may become dried out. Gifts contain different prey: Lécaillon (1905) found a gift containing two insects, one partly eaten, the other a still living curculionid. I collected in the evening a densely woven gift containing a living larva (Diptera: Syrphidae), whose heart was still beating (Nitzsche,

1987: 36, 334). In the field I found males with gifts ranging from small to medium size (2.5–42.5 mm³), mostly wrapped, containing up to three prey items and remains (Nitzsche, 1988: 358–359, summary of data of other authors). Gifts containing several prey items were also described by Homann (1931: 57) in the laboratory, where he observed the pursuit of small flies, and the wrapping of them together. After adding a fly (*Lucilia* sp.) to a gift-carrying male, in most cases the gift was dropped and a new one was produced by wrapping the fly (Nitzsche, 1987: 86–87). However, sometimes the old gift and the fly were bitten simultaneously or the gift and the fly were stuck together (compare Nitzsche, 1988: 366), so that by the next day some males had produced double gifts (analogous to winning the gift of a rival, this paper). Mating is possible with very small gifts consisting of only one wrapped fruitfly, flies or crickets of medium size, but also with very large gifts such as double gifts, consisting of two greenbottle flies, a wrapped adult house cricket, or even a blowfly (Nitzsche, 1981, 1987, this paper; Lang & Klarenberg, 1995; Stålhandske, 2001a). However, there are some problems with using very small gifts, e.g. short insertions resulting from bites in the third leg or the unused male palp. Moreover, matings are often shorter, caused by the fact that the female may finish consuming the gift before the male is able to insert both palps for a longer time. Very large prey are difficult to handle, or may be too big to be carried or are unsuitable as a gift (see semi-natural conditions, this paper). Males also differ in size (Nitzsche, 1987: 26–29; Lang & Klarenberg, 1995); larger males should be able to carry larger prey for longer, and unlike smaller ones they are able to produce densely woven gifts, because there is no adjustment of silk production in relation to prey size (Lang, 1996). Thus a given male may densely wrap a very small prey, but a large one will be wrapped more loosely. Densely wrapped prey prolongs the feeding time of the female during mating, thus enabling the male to copulate for longer (Lang, 1996), whereas unwrapped gifts often tear and are won by females without copulation (see above).

Not only the size but also the form of the gift is important for a male: a round gift (house fly) enables longer copulations than an oblong one (wrapped mealworm) (Andersen *et al.*, 2008); however, perhaps the female can qualitatively distinguish these two prey types. Females, especially hungry ones, mostly win gifts at the end of mating. Only then does she gain the lion's share of the gift (Nitzsche, 1988), and is able to ingest a large proportion (mean: 75%, up to 95%) of a freshly caught prey (Lang & Klarenberg, 1997).

All in all, a gift consisting of for example a freshly caught wrapped greenbottle fly seems to be optimal for the male (and for a hungry virgin female), because it enables him to mate for a long time and to insert several times while she is feeding.

Mating without a gift

Many authors have stated that males without gifts: (1) would be killed by females (Menge, 1879: 508;

Bristowe & Locket, 1926; Spassky, 1935; Bristowe, 1958); (2) other authors wrote that matings without gifts would not happen, because unwilling females turn away and hide or simply do not accept insertions (Van Hasselt, 1884; Gerhardt, 1923: 29; Thomas, 1928; Le Pape, 1972: 23; Austad & Thornhill, 1986); (3) injuries may also occur, e.g. Schmidt (1955) described a bite in the palp of a male, which died but was not eaten by the female. I also observed bites, but not causing death, in one third leg, the uninserted palp and the prosoma of the male. All copulations I observed under semi-natural conditions took place with gifts. (4) However, under restricted conditions in the laboratory I recorded insertions without prey items in a relatively high proportion of cases, after males had first tried to find a prey item or any object suitable for producing a gift (this paper). Also, half of Danish males (Stålhandske, 2001a) succeeded in copulating within 60 min after the first contact with the female, but insertions started significantly later than in the groups with medium and large gifts, and in all cases the female terminated the mating. Contrary to the results for German and Danish *Pisaura*, Prokop (2006) obtained different results for his spiders from western Slovakia: no female which had just mated with a gift-offering male accepted a male without a gift, and only 10% of virgin females accepted giftless males and mated for only one or four minutes, when one giftless male was killed by the female. In Prokop & Maxwell (2009) neither starved nor fed females accepted males without gifts. Therefore, the authors discussed differences between spider populations, especially the less abundant prey in the north, as demonstrated by a biennial life cycle (overwintering twice before maturation in Denmark, Lenler-Eriksen, 1969) compared with the annual cycle for *Pisaura* in Slovakia (Buchar *et al.*, 1989), as possible causes for these differences in the mating behaviour. In southwestern Germany I interpreted the life cycle as mostly biennial, compared with an annual cycle in southern France (Bonaric, 1974; Nitzsche, 1981: 29–32; literature and overview for Europe see Nitzsche, 2007: 54–58). I wonder whether the life cycles at these three localities really make a difference; probably individual differences should be considered first as the causes of different behaviour.

I recorded some special behaviours in matings without gifts: the male beats the female with his front legs, and sometimes males try to insert on the prosoma of the female instead of on the opisthosoma (this paper). Schmidt (1980: 54–58) observed insertion attempts between the chelicerae of the female, and Stålhandske (2001a: 696) also mentioned the male's difficulties in reaching the female's epigyne.

The percentage of males with versus without gifts encountering females with or without prey/gift in the field is still unknown. However, the normal way is probably for a male with gift to encounter a female without prey, because of the small proportion of prey-carrying pisaurids (adult males excluded) (Nitzsche, 1988), the production of gifts by males even without any contact with females or their draglines (Leighton, 1969), and the carrying of gifts for several days

(Nitzsche, 1987, this paper). If a *giftless* male encounters a female, first he looks for prey or a substitute; or he may meet a rival and steal his gift, or he may try to insert without a gift.

In the Japanese species *Pisaura lama* Bösenberg & Strand, 1906 and *Perenethis fascigera* (Bösenberg & Strand, 1906) matings with gifts were also the rule (Itakura, 1987, 1998). Only one female of *Pisaura lama* allowed a giftless male one insertion of 19 minutes, and she killed him at the end. However, only a few individuals were observed, 7 pairs of *Pisaura lama* and 3 males and 5 females of *Perenethis fascigera*, too few for making general statements about the behavioural variations within these species. Unlike pisaurids and trechaleids, the prey of the autumn spider *Metellina segmentata*, caught by the female web, bitten and wrapped by her, is not a male nuptial feeding strategy but only a trigger for the male's courtship; females do not feed during copulation and regain the prey with or without mating (Prenter *et al.*, 1994c).

Females with prey, with egg sacs and on nursery webs

Sometimes a *P. mirabilis* male (with or without gift) may meet a female feeding on her prey or the gift of another male. Schmidt (1952, 1955, 1980) and Nitzsche (1981, 1987, this paper) described what happens in the laboratory. Schmidt (1955: 566) observed males without gifts biting the female's prey and males with gifts dropping them. The female may even discard her prey (or remains?) and bite the male's gift (Schmidt, 1952, 1955). Males without gifts copulated significantly more frequently with females with prey than did males with gifts (Nitzsche, 1987: 191–193).

As described here, males offer their gifts even to females with egg sacs (see also Nitzsche, 1987: 133), and short insertions may follow, but there were no offspring in the next egg sac. In the field, matings with egg-sac carrying females, females that have produced their first cocoon and females on nurseries with spiderlings may be rare because of the shorter life span of males (Nitzsche, 1987: 24–25), but the last two possibilities can occur (Pénicaud, 1979: 51–52, 58). I also found a male on 9 July with a fresh gift near a nursery web (Nitzsche, 1987: 32). In the laboratory, emaciated females accept these gifts. But do these matings result in spiderlings hatching in autumn? In the laboratory females produce up to five egg sacs, and offspring can result from a single mating in up to three egg sacs (Nitzsche, 1987: 173, 181–185, 188). The statement of Austad & Thornhill (1986) for southern England, that *P. mirabilis* is “semelparous in the strictest sense”, i.e. that it reproduces in a single episode, seems to be incorrect, because a third peak in the authors' fig. 1 could be interpreted as a second egg sac, and perhaps more importantly, these authors only worked from May until the end of July. What about August and September? Pénicaud (1979) found in Brittany in 1977 only one peak in numbers of nurseries, but in 1978 also a second lower peak in the middle of September (more details see Nitzsche, 1987: 267–277). Schmidt (1952) in northern Germany found females

still carrying their egg sacs in September (my latest record: 18 October, Nitzsche, 1981: 31), and he observed matings on nurseries with spiderlings. Pénicaud (1979) in Brittany saw courtship and Austad & Thornhill (1986) in southern England also saw matings on nursery webs.

Females and males of different sizes

Males and females of *P. mirabilis* do not differ in length of tibia IV and tibia–patella, but females are larger than males in body length, mass and prosoma width (Nitzsche, 1987: 25–28; Lang, 1991; Drengsgaard & Toft, 1999, Stålhandske, 2001a; Prokop, 2006). However, more importantly for mating, there are smaller and larger individuals in both sexes, resulting from their maturing in different instars (Nitzsche, 1981: 25–28, literature therein) and perhaps caused by different feeding and light conditions, since females caught as adults in the field were larger than females reared in the laboratory (Nitzsche, 1987: 26). Austad & Thornhill (1986) found mainly larger females in southern England and interpreted this result as suggesting that the larger females ate the smaller ones or displaced them. The females I caught in the field were larger, laid more eggs and produced more spiderlings than females reared in the laboratory (Nitzsche, 1987: 179–185; see also Stålhandske, 2001a). Larger males are able to produce well wrapped gifts out of larger prey (Lang, 1996), which enables them to achieve longer matings with multiple insertions of both palps, and they mostly win fights for gifts and chase away smaller rivals (this paper). Therefore, large males and females seem to be optimal and favoured by natural selection. However, there seems to be a counter-selection against over-large males, because females copulate longer with relatively smaller males and win their gifts more often (Prokop, 2006). Longer insertions increase reproductive success, i.e. result in more fertilised eggs and more spiderlings (Nitzsche, 1987: 186–194; Drengsgaard & Toft, 1999; Stålhandske, 2001a).

Factors influencing mating duration — long versus short insertions

In the field, mating of *P. mirabilis* is terminated not only by the female, the male or other males and insects, as observed under semi-natural conditions (this paper), but also by other spiders, predators, weather factors, e.g. showers and gusts of wind, and last but not least by human disturbance. We do not know the reason for the long insertions in *P. mirabilis* compared with the very short ones of *Dolomedes fimbriatus* males. *Pisaura mirabilis* males also may insert for just a second (without producing offspring) and are able to ejaculate rapidly, even in front of an unwilling female with his palp resting on heather (Schmidt, 1955: 566; this paper). Fertilisation is possible after a short insertion, the shortest that produced offspring in the first egg sac lasted only 0.5 min, but more females produced offspring with longer durations, and the percentage of fertilised eggs was widely spread, from 6.9 to 100% (Nitzsche, 1987:

186–194). However, within 18 minutes all eggs of an egg sac can be fertilised (Drengsgaard & Toft, 1999). Matings with suboptimal nuptial gifts (small, unwrapped) and disturbed matings, which often result in short insertions, because the females run away followed by separation of the pair or dragging off the male, may also result in fertilisation.

Number of matings in the field

Austad & Thornhill (1986) saw both males and females copulating with more than a single mate during the course of the season. Thus, *P. mirabilis* is a promiscuous species, i.e. a male may mate several times with the same or different females, and a female may mate several times with the same or different males. The term “polyandry” used by Prokop & Maxwell (2009) is therefore not entirely correct. In the laboratory I recorded matings of females up to eight times before the first egg sac, and several times after an egg sac was abandoned or on the nursery web (this paper). Gerhardt (1924: 91) observed two females mating three times. Schmidt (1952) saw females copulating up to four times, and added that males are capable of mating until their death; one of his males mated 10 times (Schmidt, 1980: 58).

The willingness of the female to mate depends on her hunger level (Le Pape, 1974; Bilde *et al.*, 2007; Prokop & Maxwell, 2008). After mating twice more eggs hatched within an egg sac than after mating only once (Drengsgaard & Toft, 1999). It is not known whether a male is able to distinguish his own sperm from that of a rival in the seminal receptacles of the female, but in any case it makes sense for him to copulate with any female. Females are able to produce offspring by mating after having laid a first infertile egg sac (Nitzsche, 1987: 184), and at least some females produced a second egg sac in the field (see above) in a season when only a few males may have survived. Note that a virgin female can produce spiderlings in two egg sacs from a single mating (Nitzsche, 1987: 181–185; Drengsgaard & Toft, 1999; Stålhandske, 2001a).

4. Agonistic behaviour, aggression and sexual cannibalism

Agonistic behaviour, fights for gifts and guarding

In this paper the first data about agonistic behaviour of *P. mirabilis* in the laboratory and under semi-natural conditions are given. Gerhardt (1923, 1924) mentioned only disturbances of copulation by a second male and female. Many aspects need to be investigated using a larger number of males with similar status (e.g. same age, hunger, experience, more or less related) in order to obtain a better understanding.

Agonistic behaviour is known in males from many spider families (see also Nitzsche, 1987: 237–241). Males of the ctenid *Cupiennius salei* (Keyserling, 1877) try to insert in each other, then flee, but sometimes smaller males are killed by larger ones (Melchers, 1963). In the

lycosid *Pardosa amentata* (Clerck, 1757) three categories of males were found: large dominant males, sometimes dominant males, and constantly losing or uninterested males (Dijkstra, 1978), as in *P. mirabilis* (this paper). All in all, in most cases the larger males or the males with the strongest fighting abilities win (recent literature discussed in Huber, 2005: 371), but smaller males may be successful using alternative mating strategies. However, there are some differences between *P. mirabilis* and species in other families where, first, ritualised behaviour often exists, e.g. males grasp the chelicerae of the rivals (Foelix, 1996: 200–203): (1) As far as is known, *Pisaura* males do not have any specific morphological structures or behaviour for male–male encounters, but perhaps they possess some as yet unknown modifications of their legs and chelicerae (structure, length) for stealing the gift from their opponent; (2) A more important difference from most other spider species is the presence of the nuptial gift. Struggles for and the stealing of gifts may also occur in other pisaurids which use nuptial gifts (known species listed at the end of this paper). In the tetragnathid *Metellina segmentata* the stronger male evicts his rival from the female's web (Schmidt, 1986); the smallest males mate with small females in poor habitats, whereas the largest males move within aggregations of larger females and mate with many females, while medium-sized males within aggregations have more problems in mating (Rubinstein, 1987). In this species males guard larger females, i.e. those with more fertile eggs (Prenter *et al.*, 1994c). Under my experimental conditions some *P. mirabilis* males guarded females by chasing away rivals, but the surely more complicated situation in the field is still unknown. Fleeing males, when chased away by a rival, run the risk of being caught by females, because they do not show any sexual excitement. In a fight with a rival a giftless male may win a gift. Thus, a giftless male gains a gift without lurking or searching for prey, carrying and wrapping it; and a male with a single prey gift is able to enlarge it by wrapping both together. The stealing of a gift by a rival is one source of double or multiple gifts found in the field (Nitzsche, 1988), besides multiple prey capture or the adding of freshly caught prey to older prey or gift remains, produced by the female's or male's feeding. Robbing also occurs in the linyphiid *Oedothorax gibbosus* (Blackwall, 1841), but of secretions produced by special glands in the "head" region (gustatorial courtship, references in Huber, 2005: 367) by conspecific and even heterospecific males (Vanacker *et al.* in Huber, 2005: 368). Heterospecific robbing could also occur in different pisaurid and trechaleid species with nuptial gifts living together in the same region and habitat.

Disturbance of a pair: As shown in this paper, a second male may end or interrupt the copulation of a pair by jumping at them. However, often a second male seems unable to identify his rival or to recognise the mating, because he may simply offer his gift or grasp the gift of the pair, as observed in giftless males courting feeding females. This non-aggressive behaviour of the second male is a further indication of the inability of this species to perceive forms (see above). Not only a second male but

also the female may interrupt or terminate the mating by making aggressive movements or by simply dropping the gift with the two males hanging on it; the males may then carry the gift and attempt insertions on each other. In other pisaurids which use gifts (see below) there may be behaviour similar to that in *P. mirabilis*. In other spider families males also hinder rivals in insertion or shorten their copulation, e.g. Melchers (1963) saw a male *Cupiennius salei* shaking off a rival, which tried to insert.

Pseudo-female behaviour: Steven Austad (pers. comm.) twice observed a male presenting his gift to another, preyless male in the same way as to a female. The second male then stole the gift as soon as the first male tried to insert his palp. Thus, Austad thought that males were performing "pseudo-female-behaviour" as a strategy for prey theft. I observed struggles for gifts, robbery and male–male pairs (this paper). However, a male may not really behave as a female but possibly a male cannot distinguish another male from a female by his chemotactile senses, especially in an environment soaked in female pheromones. Thus, he may recognise a rival only by his vibrations, especially by the heavy jerking before an insertion attempt, as my observations showed. The possibility of homosexuality can be eliminated for my males, because they copulated with a female in the same experiment. Melchers (1963) also observed two males of *Cupiennius salei* trying to copulate with each other.

Aggression and cannibalism

As in most spider species, immature and penultimate stages of *P. mirabilis* may catch each other, but they are spatially separated by their way of living in webs (Leighton, 1969). In addition to killing, there are different degrees of aggression, e.g. bites in legs, both between and among the sexes (for males see above under agonistic behaviour). Usually, females are not aggressive and do not kill males, but a few do so. On the other hand, satiated females, especially when mated, do not accept gifts (Le Pape, 1974; Prokop & Maxwell, 2009); they turn, run away and hide. Thus, females have to be hungry in order to mate, resulting in high population densities in many places. Even in small boxes sexual cannibalism is rare, occurring in only 1.2–4% of encounters (Van Hasselt, 1884; Schmidt, 1952, 1955; Nitzsche, 1981, 1987; Austad & Thornhill, 1986; Drengsgaard & Toft, 1999; Stålhandske, 2001a; Bilde *et al.*, 2006, 2007; Hansen *et al.*, 2008). I observed cannibalism three times before mating (during unexcited locomotion), i.e. premating sexual cannibalism, and once after only short insertions during mating. Likewise, all killing of males by females observed by other recent authors (Drengsgaard & Toft, 1999; Bilde *et al.*, 2006) occurred before mating. Hansen *et al.* (2008) found that non-virgin females are more aggressive than virgins, this being consistent with the observations of Schmidt (1950 unpubl. in Nitzsche, 1988), who observed females in the field first with gifts, but a few days later with males in their chelicerae. Under my semi-natural conditions with only a few individuals no male was caught by a female

(this paper). Usually the killed male is eaten by the female, but once Schmidt (1980: 56) saw a female killing a giftless male during mating, but not feeding on him. Sometimes it is the struggle for the possession of the gift that causes the death of one of the sexual partners, thus the gift itself may cause cannibalism (Austad & Thornhill, 1986). Usually the female wins the gift (Nitzsche, 1987: 154–156; Stålhandske, 2001a). Males may catch old and weak rivals in the field, wrap them with silk and mate with these gifts, as observed in the laboratory (Nitzsche, 1981: 146–147). The same is known for *Metellina segmentata* males: they may wrap inferior rivals and use them during courtship (Gerhardt, 1926: 58; Bristowe, 1929: 320; Schmidt, 1986), but this is not the rule. Gerhardt observed in the laboratory a fight between two males of *M. segmentata*: the winner wrapped his killed rival and added him to a fly, thus producing a double prey comparable to the double gifts described above. *Pisaura mirabilis* males may even catch and wrap unwilling females, thus forming gifts (Austad & Thornhill, 1986; Prokop & Maxwell, 2008). Not only adult females but also immature females were killed by *Metellina segmentata* males and wrapped or eaten (Schmidt, 1986).

Summarising, the generalisations “female catches giftless male” or “hungry female/non-virgin female kills the male” are incorrect for *P. mirabilis*. There are individual differences, e.g. differences in size, more and less aggressive females and males. In general males are not killed by females and vice versa, but sometimes males with or without gifts are caught by females, depending on hunger and prey availability, female mating status, the relative size and state of health of both sexes, and probably further yet unknown factors.

5. Why do males wrap prey?

The nuptial gift of *P. mirabilis* consists of two parts, the nucleus of prey inside and a covering of silk. The female ingests both after having won the gift, but during mating the silken cover of the discoloured feeding area is not damaged, as shown by SEM photos (Nitzsche, 1988). Moreover, the amount of silk used by males for wrapping different kinds of flies is very small (mean 0.05 mg dry weight: Lang, 1996); thus, even if the female ingests the entire silken covering of the gift, this would be irrelevant for her as food.

Why do males wrap their prey and produce densely woven nuptial gifts, if mating is also possible with unwrapped prey? There must be some substantial advantages in using wrapped prey, because there are also costs, i.e. energy, time and the quantity of not unlimited silk (Lang, 1996). Spiderlings and females also wrap prey, after catching large prey or several small prey items (Nitzsche, 1981, 1988). In 1979 (Nitzsche, 1981) I discovered this “post-immobilisation wrapping of prey” of immature stages and females of *P. mirabilis* that fixes prey items to the substrate, thus preventing their loss during periods of rest and grooming. This enables the spider living within the herbaceous layer to feed on large prey items and to exploit the high input of small prey

items without the risk of losing them. Males fix their prey items and gifts with silk to leaves and stems for the same reason, e.g. after winning the gift at the end of mating and before sperm web construction. Unlike the females and immature stages, males wrap their prey items more frequently and with more silk, thus producing densely woven white nuptial gifts (Nitzsche, 1988), and they do this even if isolated and without any sexual excitement (Leighton, 1969; Nitzsche, 1981: 97–103).

Many functions of the silken gift cover have been discussed by various authors (Lang, 1996; for more details and review see Nitzsche, 2007: 239–242; Andersen *et al.*, 2008), and several are probably true. Gifts are produced by males without any contact with females (Leighton, 1969), or by sexually aroused males in the same way as immature stages and females (Nitzsche, 1988), but with reinforcement in the third part of the process (phase III, Nitzsche, 1987: 58–68), thus producing densely woven gifts, even of long-legged and winged prey items, (1) which are suitable for carrying in the herbaceous stratum and (2) do not prevent access to the female’s epigyne (Nitzsche, 1988; Andersen *et al.*, 2008; this paper). (3) Lang (1996) recorded a longer feeding time for small gifts (head of a *Lucilia* sp.) with a larger amount of silk. H. M. Peters (pers. comm.) found that Uloboridae obtain a greater benefit from their food by the silken envelope around their prey. Perhaps the silken covering of *P. mirabilis* gifts may prolong the external part of digestion, based on the fact that during mating the envelope of the gift is not dissolved; however later, when discarded by the female, only inedible silkless remains are left, i.e. the female digests the silken envelope of the gift (Nitzsche, 1988). Furthermore, the silken envelope (4) enables the female to bite into gifts made from hardened prey remains or blossoms (Nitzsche, 1987, 1988; this paper), and (5) enables the male to get a good grip with his third legs during mating (Andersen *et al.*, 2008), which can be advantageous for winning the gift during separation. Thus, the silken cover of the gift reduces the risk of it being stolen by the female by enabling an additional special male behaviour, i.e. fast biting of the gift and allowing himself to be carried away by her, the so-called “feigning death” (Nitzsche, 1987; Bilde *et al.*, 2006; Andersen *et al.*, 2008; Hansen *et al.*, 2008; this paper). The silken envelope also (6) prevents the gift breaking up during a struggle for it; if it breaks the situation is suboptimal, the female with one part of the gift and male with the other part. However, subsequent copulation is possible if the female discards her part of the gift or if the male waits until she has fed; his remaining gift part will then be accepted by her. Moreover, the silken cover of the gift may have further functions: (7) it could prevent too rapid dehydration during transport and conserve the sometimes still living contents. Males may possess special glands which produce preservative substances added to silk for gifts, thus making them long-lasting, an antibiotic function that perhaps spider silk may have per se. (8) There may also be male pheromones, which attract the female at close range, i.e. when she extends her palps just before grasping the gift with

her chelicerae (this paper). (9) There could also be chemical substances in the silken cover of the gift, sensed by the female's palps during feeding and dissolved by her digestive juices, which might tranquilise her or encourage her to mate. Note the struggles by females for possession of the small gifts of wrapped *Drosophila* and wrapped heather blossoms at the end of matings (this paper), and the fact that unwrapped flies are more often stolen without mating (Andersen *et al.*, 2008).

6. Functions of nuptial gifts

Shelter from female

In older literature and some new spider books, the gift has been suggested to function as protecting the male against female aggression and cannibalism, preventing him from being eaten by her during mating, because it could distract her from him. In the laboratory the male is usually not endangered, but sometimes a female may kill a male with or without a gift before mating. In such cases when the female attacks him, when the male in a split second turns around and lets the attacking female bite the gift instead of himself, there is a protective function, which may have been more important in the earlier stages of evolution.

Seduction by lure

Van Hasselt (1884) called the offering of wrapped prey "verleiding" (seduction) of the female by the male. His male, kept together with a female for a long time, was larger and nimbler, so he caught more flies, and one day the hungry female suddenly jumped down to him, bit the gift and greedily started to feed. Thus, Van Hasselt called the gift "lookas" (lure). A well-known similar behaviour is the necessity for prey to be present in the web of the tetragnathid *Metellina segmentata* to initiate courtship. Contrary to earlier authors, Blanke (1974) observed that the prey used for courtship was captured by the female and then during the post-immobilisation wrapping process stolen by the male, which beats the female, especially with his first pair of legs, until she flees and leaves the prey to him. This resembles the beating of the female by a giftless *P. mirabilis* male (this paper). In *Metellina* the wrapped prey functions also as a lure and enhances the male's courtship success.

Mediation and orientation, male mating effort and female's foraging motivation

Once I referred to the nuptial gift of *P. mirabilis* as an "object of mediation" (Nitzsche, 1988) for mating and additional nutrition for the female that seldom serves as a shelter against female attacks and which could become food for the male, and discussed further explanations (Nitzsche, 1987, 1988, 2007). Recently the function of the gift has been considered mainly as a "male mating effort", i.e. the wrapped prey enables the male to copulate with the female for long enough to transfer sperm (Pfeil *et al.*, 2001; Stålhandske, 2001a; Prokop &

Maxwell, 2009). The rounded gift enables him to orientate to the female's epigyne: when sitting in a vertical position he has only to move upwards to reach his destination (Stålhandske, 2001a; this paper), whereas males with freshly caught, relatively large unwrapped prey items such as flies may have problems orientating (this paper). Problems also arise with large ellipsoid gifts (Andersen *et al.*, 2008), but larger gifts enable longer-lasting insertions, copulations and mating than smaller ones and result in fertilising more eggs (Nitzsche, 1987; Drengsgaard & Toft, 1999; Pfeil *et al.*, 2001; Stålhandske, 2001a). Thus, the female's foraging motivation maintains the nuptial gift behaviour (Bilde *et al.*, 2007). Nuptial gifts are "additional food" to females, and provide nutritional benefits; normally, they contain prey enclosed in a densely woven silk cover, i.e. proteins, but may also contain only prey remains or different kinds of prey than females catch, based on a different hunting strategy, i.e. searching and feeling instead of sit-and-wait and jumping (Nitzsche, 1988, this paper). At present it is unknown how many gifts of what quality a female may receive and feed on between her last moult and producing her first egg sac. Furthermore, we do not know the amount of food females obtain by their own prey hunting, which may include smaller females (this paper; smaller ones disappear in the field: Austad & Thornhill, 1986) and males. The amount of time females save by accepting gifts instead of lurking for prey is also unknown. There may be considerable differences within populations (density of potential prey and of *Pisaura*).

Males mature earlier than females in the field (Stålhandske, 2001b). It is not known whether the male waits for the female's last moult, already well prepared with a gift in his chelicerae, or whether some males guard females in nature, as observed in the laboratory. If they do, a single male could be the father of all or most of the offspring of a single female. If he "feeds" her and exclusively mates with her, especially for her first time, because of first sperm priority his gifts would be a real "paternal investment". In other spider species, where sexual cannibalism is frequent (e.g. *Argiope bruennichi* (Scopoli)) and the smaller males themselves are the most extreme form of nuptial gift, the consumption of one or two males did not result in any fitness benefit for the female (clutch number or size, hatched eggs) but in prolonged insertions (Fromhage *et al.*, 2003). In this case, males are not a paternal investment but only additional food for females; perhaps the gifts of *P. mirabilis* serve a similar function.

7. Evolution of gifts

Mating without a gift is the primitive form, and males of *P. mirabilis* without gifts are still able to insert their palps for a short time and produce offspring (this paper). Mating with a nuptial gift is a derived form of mating and is now the normal way in this species and its kin (see below) and is certainly genetically fixed. Gifts are used in all populations, although there may be some local differences in the proportion of females mating without a gift or with unwrapped prey (Prokop & Maxwell,

2009). In my monograph (Nitzsche, 2007: 243–253) I presented a review of ideas found in the literature since the beginning of the last century (Lécaillon, 1905) and added my own ideas (Nitzsche, 1981: 199–203; 1987: 250–254) about how the nuptial gift of *P. mirabilis* could have originated and evolved. I discussed its origin in the context of “post-immobilisation wrapping” of prey in both sexes and all stages. Probably all pisaurids (and trechaleids?) are inhabitants of the herbaceous layer (at least for a part of their life), and all stages and both sexes developed “post-immobilisation wrapping” as an adaptation against prey loss in this stratum. Austad & Thornhill (1986), concentrating on the prey part of the gift, gave a possible scenario for its evolution, and concluded: “why, if it is so beneficial for both sexes, has nuptial feeding behaviour not evolved in other spiders?” Now, we know gifts occur in several pisaurid and trechaleid species, but not in all pisaurid genera (see below). The problem is to decide when males began carrying prey (with the aid of only a few threads). Perhaps there were hungry aggressive females within dense populations which obtained more food and sperm than other females by biting and feeding on the male’s prey instead of the male. If so, when and where did this occur?

Males of other species drop freshly caught prey after contacting females, e.g. *Dolomedes fimbriatus* (Nitzsche, 1987: 168–170). After feeling for the male’s prey by the female of *P. mirabilis* became established, selection pressures for larger prey items, enlargement of gifts by capturing further prey or stealing the gifts of rivals, and a denser silken cover would have operated. Females may be able to select males indirectly by the quantity and quality of the offered gift (kind and state of prey inside, silken cover) after having felt it with their palps and during feeding, and allow insertions for different durations. Female selection would result in relatively large and fit males, i.e. good hunter-gatherers with strong venom, capable of catching and collecting prey. Austad & Thornhill (1986) found that smaller females in the field did not survive the hunger period during egg-sac carrying; larger females produced more eggs and survived long enough to guard high numbers of offspring from 1 or 2 fertilised egg sacs. More feeding produces earlier egg sacs. Therefore, evolution favours strong large females, capable of catching large prey. Selection also favours large males capable of catching large prey and wrapping it more densely than smaller rivals (Lang, 1996), carrying it for a considerable distance and time, enlarging it by adding further prey items, and chasing away smaller rivals (this paper). On the other hand, females seems to favour *relatively* smaller males, i.e. they allow them longer copulations, thus selecting against males that become too large (Prokop, 2006). Anyway, females select males and their fitness first by acceptance of their gifts and secondly by their acceptance of longer or shorter insertions. In addition to simple sperm storage there may be some unknown internal mechanisms by which the female allows certain parts of the sperm and/or sperm deposited in the right or left spermatheca to fertilise her eggs during oviposition (“cryptic” female

choice, see Schneider *et al.*, 1998). Today males accept different sorts of prey items, even substitutes, as cores for their nuptial gifts and wrap them normally with a dense layer of silk. There is, therefore, every indication that there exists a strong pressure (1) to have a gift, and (2) to enlarge it by adding further prey or the gifts of rivals (Nitzsche, 1988, this paper). Larger gifts enable longer insertions (Stålhandske, 2001a) and a higher fertilisation rate of eggs (Stålhandske, 2001a), i.e. from the male’s perspective a higher degree of paternity. The size of gifts is limited by problems for males in wrapping very large prey items (Lang, 1996), and in carrying them (this paper) and, if these difficulties are surmounted, in finding her epigyne (Andersen *et al.*, 2008); the same problem occurs with unwrapped flies (this paper).

Only relatively small gifts have been found in the field (Nitzsche, 1988), mostly collected in France (Brittany: Pénicaud, 1979), Germany (western part: this paper) and Denmark (eastern Jutland: Toft, unpubl.), probably all collected during the day. What about the night, when males and females also capture prey and mate (this paper)? In southern Europe females and males should be larger, becoming adult after a higher number of moults (Bonaric, 1974), and may catch larger and different prey. We do not know how far and for how long males may carry their gifts in the field before losing them to females or discarding them when catching new prey items.

8. Mating in nature and many open questions

Only a few observations of courtship and mating of *P. mirabilis* in the field have been published (see Introduction). Austad & Thornhill (1986) in southern England never recorded matings without gifts. This is the norm, as my observations under semi-natural conditions confirmed. It is not known how often females cannibalise other females — or even males, especially in the period before egg laying, as Schmidt (1952) observed. Sometimes a giftless male may kill an unwilling female. What about the chances for handicapped males and females (after leg and palp losses?). Copulation may occur more often in the evening and at night, but the influence of the lower temperature at night on activity, courtship and mating is still unknown (e.g. average temperatures at Kaiserslautern, max./min.: May 19°C/08°C, June 22°C/12°C, July 24°C/14°C, Wikipedia). How often do females catch their own prey and of what size, probably more frequently than males? The ratio of prey caught by females versus gifts eaten during and after mating is also still unknown. Why do males produce sperm webs so often, even without mating in between? (Nitzsche, 1987: 90–101). What happens within the female to the sperm transferred by multiple matings? There seems to be first-male sperm priority, but later males also succeed in fertilising eggs (Drengsgaard & Toft, 1999). It is even unknown whether males are capable of removing the sperm of their rivals, as is known to occur in other spider species, or whether they produce mating plugs. How much of their sperm and what further substances do they transfer at which time during their long-lasting

insertions, when a few minutes are sufficient to fertilise 100% of the eggs? (Drengsgaard & Toft, 1999). Are there special glands on the male's raised palps which produce and emit pheromones to attract or calm females during courtship? Are the spinnerets and spinning glands modified to produce the dense silken covers of gifts? Do larger males guard females and mate with them, providing them with gifts stolen from rivals? Or do all males of whatever size wander and try to mate with as many females as possible in spite of the higher risk of being captured by a predator? Pénicaud (1979: 39) did not recapture any marked males, in contrast to earlier instars, possibly an indication of wandering.

9. Other pisaurids and trechaleids using nuptial gifts

In contrast to the well-known nuptial feeding of many insects (e.g. Empididae, Bittacidae, Panorpidae, for review see Vahed, 1998, for discussion of special aspects including spiders see Vahed, 2007), for a long time *P. mirabilis* was thought to be the only spider to exhibit nuptial feeding (Austad & Thornhill, 1986). However, recently further nuptial gifts of the same kind (densely wrapped prey) have been described in several species belonging to two spider families:

Pisauridae (Europe, Japan, Panama, USA): *Perenethis fascigera* Bösenberg & Strand, 1906 (Itakura, 1998, 1999), *Pisaura lama* Bösenberg & Strand, 1906 (Itakura, 1987); *Thaumasia argenteonotata* (Simon, 1898) (Nitzsche, 1987, 1988); *Timus peregrinus* (Bishop, 1924) (J. Carico, pers. comm.).

Trechaleidae (South America: Brazil, Uruguay): *Paratrechalea azul* Carico, 2005, *P. galianoae* Carico, 2005, *P. ornata* (Mello-Leitão, 1943), *Trechalea bucculenta* (Simon, 1898), *Trechalea* spp. (Albo *et al.*, 2009; Costa Schmidt *et al.*, 2008; Lapinski & Tschapka, 2009).

Thus, nuptial gifts are now known in the four pisaurid genera *Perenethis*, *Pisaura*, *Thaumasia* and *Timus*, and matings with gifts have been observed in three species (*Pisaura lama*, *P. mirabilis* and *Perenethis fascigera* [the latter may be conspecific with *Perenethis venusta* L. Koch, 1878, see Sierwald, 1997: 390]), and four trechaleids in two genera (*Paratrechalea azul*, *P. ornata*, *Trechalea* spp.). Possibly future studies may reveal nuptial gifts in all species of at least these pisaurid and trechaleid genera and perhaps in other genera as well, because so far the mating behaviour of most pisaurids (339 species in 53 genera) and trechaleids (104 species in 18 genera) remains unknown (Sierwald, 1997; Platnick, 2010).

Within the monophyletic subfamily Pisaurinae, consisting of 18 genera related to the genus *Pisaura* occurring in Eurasia and Africa (Sierwald, 1997), males of at least some species of *Pisaura* and *Perenethis* are known to produce nuptial gifts. (1) The mating of *Pisaura lama* lasts for up to five hours, as long as the gift is present, but unlike in *P. mirabilis* accompanied by steady vibrations transferred by the male's legs. Females of *P. lama* discard their own prey during mating and resume feeding thereafter. Males without gifts usually do not succeed in copulating, and are killed by females or kill

females, producing gifts of them; once a male inserted for 19 min, but was killed at the end (Itakura, 1987). (2) In *Perenethis fascigera* we find the same type of sexual excitement by leg rubbing and a similar way of mating, with multiple matings and different mating durations with different kinds of gifts (prey remains vs. complete insects), as in *P. mirabilis* (Itakura, 1998). However, no giftless mating was observed, and males do not start gift wrapping before making contact with females (see also *Paratrechalea*: Albo *et al.*, 2009). (3) The mating of *Timus peregrinus* is unknown, but J. Carico (pers. comm.) encountered a male with a gift. (4) The gift of the small Panamanian species *Thaumasia argenteonotata* has a special feature: a package of silk or a ball of threads (Nitzsche, 1988, sub *T. uncatata*). This may form an additional food supply for the female, enabling the male to prolong his insertions and optimise sperm transfer, thus functioning as a male mating effort. However, its nocturnal mating has never been observed. Perhaps this species may exhibit a tendency to replace prey by silk, as known in the evolution of gifts in the Empididae (Insecta: Diptera)? What about mating in other *Thaumasia* species, and does the relationship between living in the herbaceous layer and the origin and primary function of post-immobilisation wrapping of prey exist in all pisaurid and trechaleid species? *Pisaura lama* and *Perenethis fascigera* are known to inhabit the herbaceous layer (Itakura, 1999; Sekine, 2006), which is also true for the immature stages and females with egg sacs or spiderlings in their nurseries of *Thaumasia argenteonotata* (W. Nentwig, pers. comm.). *Timus* species hunt at water margins similarly to *Dolomedes*, but immature stages and females build webs in the herbaceous stratum (Carico, 1976). Adult trechaleids hunt on the surface of water at night, but juveniles hunt on rocks during the day (Silva *et al.*, 2005); do the juveniles live at night in clefts between rocks or within the herbaceous layer as do at least some "free-hunting" pisaurids (e.g. *Dolomedes fimbriatus*, *P. mirabilis*, *Pisaurina mira*) (Lenler-Eriksen, 1969; Carico, 1985; Nitzsche, 1987)? More important for the origin of the nuptial gift is the question: do females and immature stages of all these species wrap their prey items (if they are large, the hunger level is low, or for grooming activities) as in *P. mirabilis*, *Dolomedes fimbriatus* and *Thaumasia argenteonotata*? (Nitzsche, 1987, 1988). When and in which spider species did the first nuptial gift originate, in a common ancestor of all cited pisaurids and trechaleids?

The gift production, courtship and mating of trechaleids are similar to those of pisaurids, but prey is caught on the water surface, and the male mounts the female as in lycosids, but between her first and second legs, and insertions are very short as in *Dolomedes* species (Albo *et al.*, 2009; Costa-Schmidt *et al.*, 2008). In other pisaurids silk plays another important role in mating: the male "ties" the female, i.e. wraps her legs together, in *Pisaurina mira* (Walckenaer, 1837) (Bruce & Carico, 1986, 1988), *Tetragonophthalma vulpina* (Simon, 1898) (P. Blandin, pers. comm.) and *Thalassius spinosissimus* (Karsch, 1879) (Sierwald, 1988), a behaviour also

known in *Ancylometes bogotensis* (Keyserling, 1877) (Merrett, 1988). In this context, it is interesting that giftless *P. mirabilis* males spin and fix draglines to the substrate and different parts of females, especially before insertions (this paper). Is this reminiscent of an era before the use of gifts in courtship? The use of silk by males for tying females to the ground has also been reported in some crab spiders (*Xysticus* sp.) and in *Nephila* (Foelix, 1996: 189–190). Males of *Metellina segmentata* also use silk in this manner, if females resist their courtship for a long time (Bristowe, 1929: 320; Schmidt, 1986). Contrary to these species which use silk in different ways in courtship and mating, other pisaurids mate without gifts or the use of silk (e.g. *Dolomedes*).

In conclusion, much remains to be done by present and future generations of arachnologists to reveal which species use which kind of mating. Moreover, there may be some changes in systematics. Santos (2007) writes: “The monophyly of Pisauridae is currently accepted, although not without reservations.” In his phylogenetic analysis comparing many morphological and some behavioural characters (e.g. type of egg-sac carrying, without using mating characters) he obtained trees with relationships between pisaurid genera. Sister groups are *Pisaura* and *Euprosthops*, *Tinus* and *Thaumasia*, *Pisaurina* and *Dolomedes*, *Thalassius* is isolated, and outside the monophyletic pisaurids there are the genera *Trechalea* and *Aglaoctenus*. As described above, gifts are known in *Pisaura*, *Tinus*, *Thaumasia* and *Perenethis* (not included in Santos’ tree). It would be interesting to know whether there are nuptial gifts in *Euprosthops* species, which live in large webs in the African savannah (Blandin, 1974). Revisions are necessary even for the genera *Pisaura* and *Perenethis*. Thus, at present we find 18 *Pisaura* species in the world spider catalogue (Platnick, 2010), but are they all real species and do they all mate with nuptial gifts?

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