

Courtship, egg sac construction, and maternal care in *Kukulcania hibernalis*, with information on the courtship of *Misionella mendensis* (Araneae, Filistatidae)

Gilbert Barrantes

Escuela de Biología,
Universidad de Costa Rica,
Ciudad Universitaria Rodrigo Facio,
San José, Costa Rica, CP 2060

Martín J. Ramírez

Museo Argentino de Ciencias Naturales,
Consejo Nacional de Investigaciones Científicas y Técnicas,
Av. Angel Gallardo 470, C1405DJR
Buenos Aires, Argentina

Summary

Morphological and behavioural traits place Filistatidae basally within Araneomorphae, although some features, such as their continuing to moult after reaching adulthood, are reminiscent of mygalomorph spiders. This paper describes the courtship behaviour and other aspects of the reproductive biology of *Kukulcania hibernalis* and *Misionella mendensis*, and compares this information with that from related filistatid species and with Mygalomorphae. *K. hibernalis* has some unique behaviours during courtship (e.g. male lays threads on female web); other behaviours are probably widespread within Filistatidae (e.g. male uses the tarsi and metatarsi of one of his legs to rub the basal sections of the female's legs and the sides of her cephalothorax). Some other behaviours seem more similar to Mygalomorphae than to those of other, more derived Araneomorphae. These include male construction of a large sperm web, and the positions of male and female facing each other during copulation, with the male holding the female cephalothorax lifted while insertions occur, similar to some mygalomorphs. The adult female *K. hibernalis* and the first instar spiderlings (outside the egg sac) feed simultaneously on the same prey, but spiderlings are also capable of cooperating during the attack of large prey. The courtship behaviour supports the hypothesis that places Filistatidae basally within Araneomorphae.

Introduction

The reproductive biology is relatively well known for an increasing number of species in different spider groups.

This is particularly so for mating behaviour (e.g. pre-copulatory behaviour), a topic for which a sizeable literature has rapidly accumulated, particularly on araneoids (Robinson & Robinson 1980; Eberhard & Huber 1998; Knoflach 2004; Aisenberg & Barrantes 2011) and, to a lesser extent, for other spider groups (Hebets & Uetz 2000; Straton *et al.* 1996; Uhl, Schmitt & Schäfer 2005; Barrantes 2008). However, despite the increasing research on the reproductive biology of spiders, information is still scarce, even for many common spiders (Schneider & Andrade 2011).

This is the case for the common synanthropic species *Kukulcania hibernalis* (Hentz, 1842), whose reproductive biology is very poorly known. Its pre-copulatory mating behaviour was briefly described by Gertsch (1949: p. 141) as a dance in which the male “uses [his long legs] to hold the front legs of the female as the couple parades back and forth in a prenuptial dance”, and Ramírez & Grismado (2008) also briefly described its copulatory position. The egg guarding by females and social interaction of juvenile *K. hibernalis* was documented by Curtis & Carrell (1999). The adult female maintains contact with her egg sac during the incubation period and, after emerging from the sac, the spiderlings remain closely associated with the female. Juveniles cooperate to kill prey and then feed together, but the female does not provide prey to her offspring (Curtis & Carrell 1999). Similar behaviours have been also reported for *K. geophila* (Chamberlin & Ivie, 1935) (Cokendolpher & MacDonald 2008).

Filistatids are placed as the most basal group of the Haplogynae clade of Araneomorphae (Platnick *et al.* 1991; Ramírez 2000; Coddington 2005; Griswold *et al.* 2005). They are long-lived spiders (Foelix 2011), whose females continue moulting and growing as adults, and with a copulatory posture similar to Mygalomorphae and Mesothelae (Ramírez & Grismado 2008). Based on these life history features, and some behavioural and morphological characters, some authors have suggested an even more basal position for Filistatidae within Araneomorphae (Lopardo *et al.* 2004; Griswold *et al.* 2005). Here, we describe the courtship behaviour in six pairs and the sperm web construction (one male) of a member of the subfamily Filistatinae, *K. hibernalis*, and provide additional information on the social behaviour of spiderlings. We expect that these detailed descriptions will help understand the evolution of

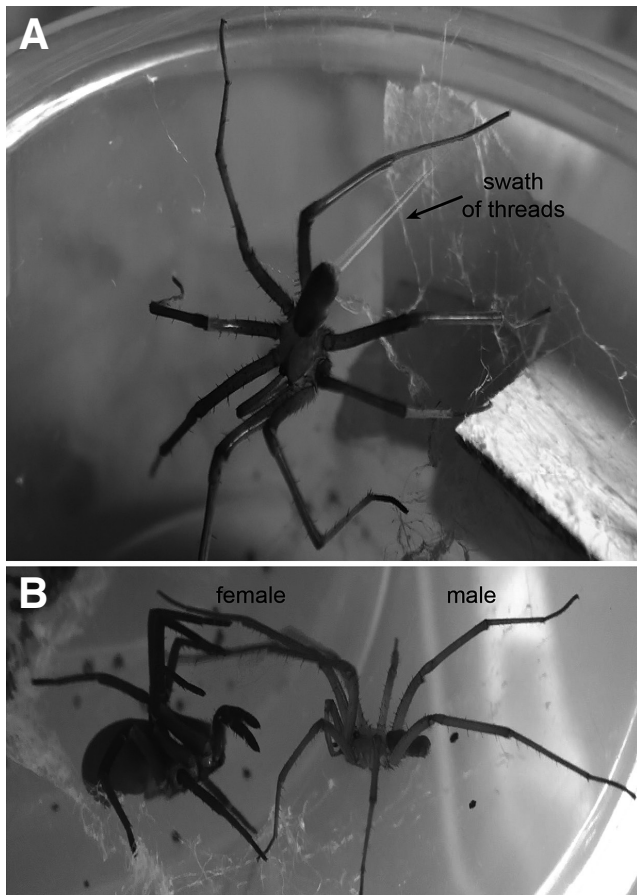


Fig. 1: Initial phases of male courtship. **A** Male laying threads on female web; **B** Male tapping female legs.

the courtship behaviour of filistatids in relation to Mygalomorphae and other closely related araneomorph groups. We also compare the courtship behaviour of *K. hibernalis* with some casual observation of the courtship behaviour of the filistatid *Misionella mendensis* (Mello-Leitão, 1920), a representative of the filistatid subfamily Prithinae.

Material and methods

Kukulcania hibernalis

We collected 12 juvenile *K. hibernalis* in the western Central Valley, Costa Rica, and raised them in captivity to adulthood. We placed each spider in a square plastic container (15 cm² × 6 cm height) that had four small rocks (c. 2.5 cm³) adhered to the bottom of the container with adhesive tape. Two of these rocks were placed at one corner, separated from each other by 1 cm; this space was used by all spiders as their retreat. We placed the other two rocks at 6 cm and 8 cm from the other two rocks and at 3 cm from the wall of the container. The spiders used these rocks as supports for their webs. We offered the spiders two prey items (e.g. flies, crickets, grasshoppers, katydids, moths) every week. Prey ranged in size from 0.75× to 1× the size of the spider, and they were collected in the field near in the same location where spiders were collected.

For observations of sexual behaviour, we paired six recently moulted virgin females, raised in captivity, and

adult males that were found wandering on buildings. Virgin females accepted males only after 2–3 weeks had passed following the moult to maturity. When we had a mature female, we searched for adult males in buildings and paired the female with the first male found. If the female rejected the first male, we paired her with a second or third male as required; each female copulated with a single male. Observations of sexual behaviour began when we placed a male on the virgin female's web at the corner opposite her retreat. We recorded courtship and copulation of six virgin females using a video camera (Sony HDR-SR11) with macro lenses (+2, +4, or +10) as needed; one of these females had moulted after laying her first egg sac (with fertile eggs). We also opportunistically observed the courtship, copulation, and egg sac construction of two adult females that were free in a house. We took pictures using a digital camera (Nikon Coolpix 4500), and compared the information obtained from these females with that obtained from the video recordings of virgin females.

We described the social interactions during prey attack and feeding of four adult females with their spiderlings, the interactions among their spiderlings, and among spiderlings that emerged from two additional egg sacs collected in the field. To describe the social interactions between spiderlings and between adult females and spiderlings we fed spiders and spiderlings with blow flies and flesh flies up to 10 times the spiderlings' size and video-recorded their interactions.

Misionella mendensis

For comparative purposes, we observed and obtained pictures of some phases of the courtship behaviour of one pair of *M. mendensis*, a common synanthropic species in northeastern Argentina and southern Brazil. Spiders were observed on the female's web on a brick wall at the Centro de Investigaciones Subtropicales at Iguazú National Park, Argentina. Photographs were taken with a Nikon F3 camera and macro lens (Nikon 105 mm) and macro flash (SB-21).

Results

Kukulcania hibernalis

Courtship behaviour

The courtship of *K. hibernalis* included five more or less distinct, consecutive phases: male deposits threads; male vibrates abdomen; male and female tap each other's legs; male hooks claws of the female; and male pulls the female. The last behaviour (described in a later section) was followed by copulation. We based the description of the courtship behaviour on the video recordings of the six pairs that copulated. However, some specific behaviours did not occur in some pairs; consequently, the sample size for these behaviours vary and are indicated in each case. Duration of the total courtship and of each phase varied substantially among pairs. In total, courtship and copulation lasted a mean of 74.09 min (sd = 59.72 min, n = 6) for virgin females and

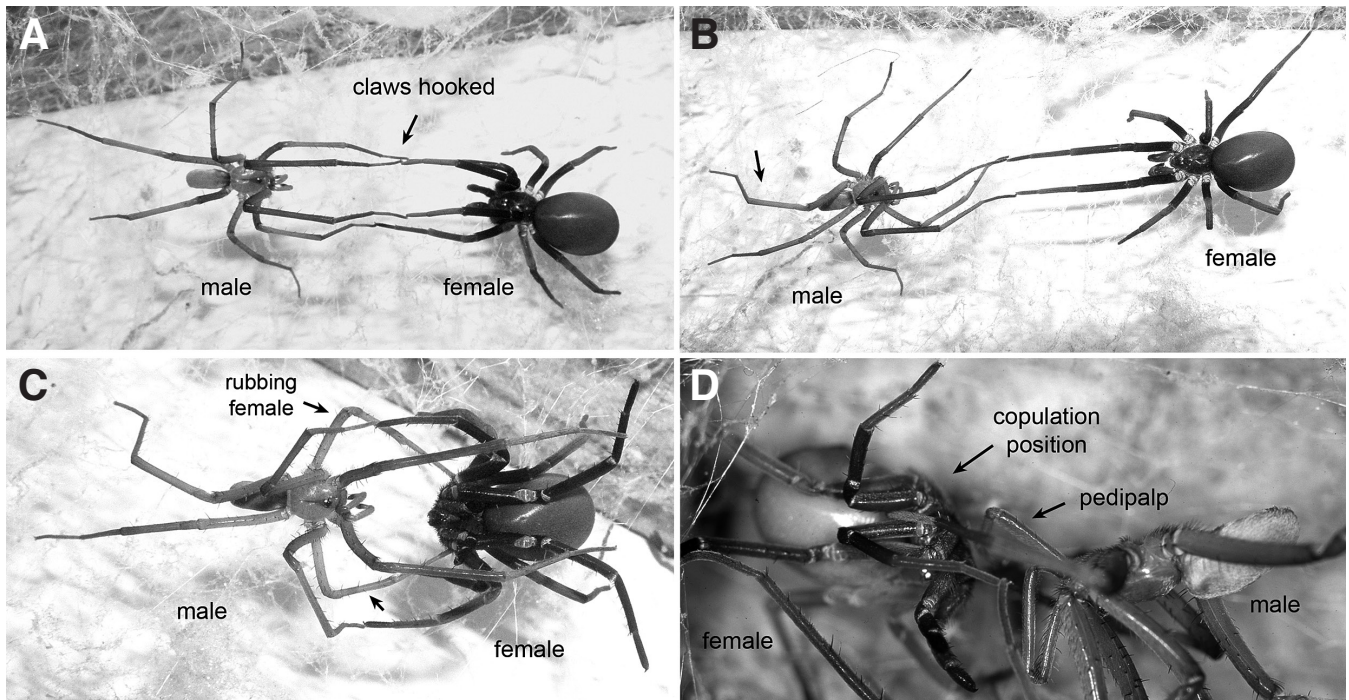


Fig. 2: Male–female courtship prior to copulation. **A** Male hooking claws with female claws; **B** Male pulling the female; note the legs of the male are bent (black arrow) as he pulls the female; **C** Male rubbing the basal section of the female's legs II, while hooking his claws of legs II with the corresponding claws of the female and holding the female's legs I with his corresponding legs; **D** Female in copulation position; note leg II of the male rubbing the lateral section of the female's body, between legs II and III.

36.50 min (sd = 30.41 min, $n = 2$) for previously copulated females.

Almost immediately after we placed a male in a female's cage, he began to add non-cribellar threads to the female's web as he walked, apparently randomly, on it. This behaviour was not seen when males walked on webs of non-receptive females or on the webs they had previously occupied. The male pulled a swath of threads with alternating movements of his legs IV that adhered to the female's web using the metatarsi–tarsi of his legs IV (Fig. 1A). The male often paused briefly and then continued walking and adding threads, or stopped adding threads, vibrated his abdomen with fast dorso-ventral movements, and then continued walking and adding threads.

Often, the male abruptly interrupted laying threads when the female reacted to the presence of the male in her web by moving inside the tunnel retreat. Five of the six virgin females reacted by moving rapidly inside her tunnel retreat, sometimes ($n = 2$ females) leaving it and launching herself toward the male. The male's reaction to female movement inside of the retreat and her attacks was highly variable among pairs. Four males froze briefly when they apparently detected the female's movements, and then continued adding threads but, on two occasions, the same male abandoned the web to return a few minutes later, after the female had returned to her retreat. In two cases the same virgin female captured and killed the courting male after a rapid attack. The third male we offered to this female seemed to intensify his courting behaviour (i.e. paying out threads and abdomen vibration) when the female launched herself toward on him, and eventually copulated with her. On another occasion, a virgin female reacted with more subtle movements, moving slowly inside her retreat and then to the retreat opening. The courting male froze at first, but then moved directly

toward the female, omitted the adding threads and abdomen vibration behaviours, and initiated the next stage of courtship, male-female leg tapping. On at least three occasions it appeared that adding threads and abdomen vibration reduced the aggressiveness of the female. In two of these cases the female had rapidly launched herself toward the male, but she stopped as the male continued to add threads and vibrate his abdomen. On another occasion, the male froze at the rapid movements of the female, but she then returned to her retreat as the male re-initiated his courtship.

After the aggressive reaction, the females eventually returned to their retreats and the males concentrated the courtship behaviour around the female's tunnel opening. Then the female began to move slowly inside her retreat (often after she had launched herself toward the male and then returned to her retreat) and slowly walked towards the retreat opening. The slow movements of the female seemed to indicate to the male her acceptance since, at this point, the male approached the retreat opening and began to tap the web by moving his legs I and II with alternate dorso-ventral movements. If the female was close to the male she responded with similar movements, otherwise she first approached the male and then began her own tapping movements. They continued approaching each other until the male's legs I contacted the female's legs. When this occurred, the female raised her legs I and II over her body (Fig. 1B). At this point, the male intensified his legs movements, first waving his legs I and II in front of her, and then tapping her legs I and II on their dorsal surfaces of her legs or, more often, sliding his tarsi distally along the posterolateral surfaces of the tarsi of the female's legs, from the base to the tip.

Hooking claws, prenuptial dance, and copulation

The long, pseudosegmented, flexible tarsi of the male's legs I and II, allowed him to slide the tip of his tarsi along the posterolateral side of the more rigid tarsi of the female's legs and hook the claws of his legs I and often of legs II with the claws of the corresponding legs of the female (often after six attempts) (Fig. 2A). His claws formed an angle of nearly 90° with the female claws as he hooked them. The two spiders then initiated the prenuptial dance. The male pulled the female towards him as he walked backwards. The female offered some resistance, and only stepped slowly forwards when the male pulled her. Often the male then pulled her harder, flexing his legs I and II, and then performed a series of short jerks with all his legs (Fig. 2B), and walked backwards to pull her again. During the dance, the male's claws often became unhooked, but he rapidly hooked them again. The prenuptial dance lasted a mean of 3.77 min (sd = 3.22 min, n = 6 pairs).

In all pairs, the male rubbed his legs III on the lateral side of the female. On two occasions, in which we had a good lateral view, we saw that the male extended his legs III anteriorly on both sides of the female and began to use the distal section of his tarsi III to rub the coxa–trochanter–femur of the female's leg III, as well as the lateral area of her cephalothorax around the base of her leg III and, less frequently, the coxa, and possibly the trochanter, of her leg II. As the male rubbed the female, the femur–tibia of his legs III formed an outward angle of nearly 90° (Fig. 2C–D). Then he often moved the femur and tibia of each leg rapidly in an extended dorsoventral movement, alternating each leg III, while maintaining contact with the female. These movements were easy to see at the femur–patella–tibia joint of the male's leg III. Only after rubbing movements had occurred did the male initiate copulation.

The female responded to the male rubbing behaviour by moving the anterior section of her cephalothorax dorsally at nearly the same time when the male extended one of his pedipalps toward her (Fig. 2D). During copulation, the longitudinal axis of her cephalothorax formed an angle of 16–19° (n = 2 females in which the angle was possible to measure) relative to its initial position. At the same time, she exposed her genital area, raising the anterior portion and/or lowering the posterior portion of the ventral surface of her abdomen. In two cases, as the female changed position, the male unhooked his claws and placed the tarsi of his legs I and II on the corresponding tarsi of the female, apparently pushing her legs over her cephalothorax. In the other four pairs, the male placed his tarsi I on her corresponding tarsi, but did not unhook the claws of legs II (Fig. 2C).

Prior to copulation, the male maintained his pedipalps with the tibia folded against his femur and both directed dorsally. With the female in the copulatory position, the male first lowered one of his pedipalps with the tibia still folded against the femur in front of the female, with the two segments directed under the female's body, and then he extended the tibia at the same time that he gradually rotated the femur medially 180° at its articulation with the trochanter, so that the tibia–tarsus joint pointed ventrally (relative to male's body) and the tip of the pedipalp was directed dorsally. The male then extended the pedipalpal

bulb, made a few flubs (the bulb rubbing the female genital area without engaging it as in a successful insertion) near the female's genital opening, then the tip of the embolus seemed to hook into the opening and copulation occurred. During copulation, the posterior tip of the female's cephalothorax projected ventrally. In this position, the tip of the cephalothorax apparently serves as support for the male's pedipalp as he searched for the female copulatory orifice. During copulation, the anterior margin of the male's cephalothorax was near the female's chelicerae.

In this position, the male continued to rub the tarsi of his legs III on the basal segments of the female's legs III and II, and on the lateral surface of her cephalothorax; in addition, he often replaced his tarsi III on the base of her leg IV. The insertion of each pedipalp lasted only a few seconds (mean = 4.04 s, sd = 2.26 s, n = 8 insertions in 5 males); no haematodochal inflations were seen. The male inserted the second pedipalp without changing copulatory position and, in all cases, continued his rubbing behaviour. After copulation, the male released the female rapidly. She remained immobile for 2–5 seconds, but then attacked the male if he still remained in her web. In one pair, the female moved her body and legs I and II forwards and the male tried to maintain her in copulatory position using his legs and one of his pedipalps. As she continued to push, he released her and moved away while she maintained an aggressive position similar to that for prey attacks (Barrantes & Eberhard 2007).

Variation in courtship

Males did not add threads when courting one virgin female and two copulated females. Each of the copulated females had already begun egg sac construction when the male walked into her web. The male walked slowly into the female's tunnel, pausing often and vibrating his abdomen, and the female interrupted the construction of the egg sac and walked slowly along the tunnel toward the male. Once they were close, the male began leg movements (tapping phase) and courtship continued with the other phases.

Sperm web and sperm induction

One male constructed a sperm web and charged his pedipalps some minutes after having initiated the thread addition phase of the courtship. The scaffolding of the sperm web consisted of nine threads, a pair of which was nearly parallel, and was constructed near the entrance of the female's retreat (Fig. 3A). After the male laid the first five threads, he descended from this scaffolding, walked for about six seconds on the female web, and then went back to the scaffolding and continued adding the other four threads; construction of the scaffolding lasted 3 min 12 s. He then walked a few millimetres along the nearly parallel threads and began to lay a wide swath of threads between the two parallel threads. He used only his spinnerets to fill a portion of the length of the parallel threads as long as his body length with silk (Fig. 3B and D). The male laid the swath of threads on the parallel threads following a zigzag movement of his abdomen. His movements were not always forwards, and he

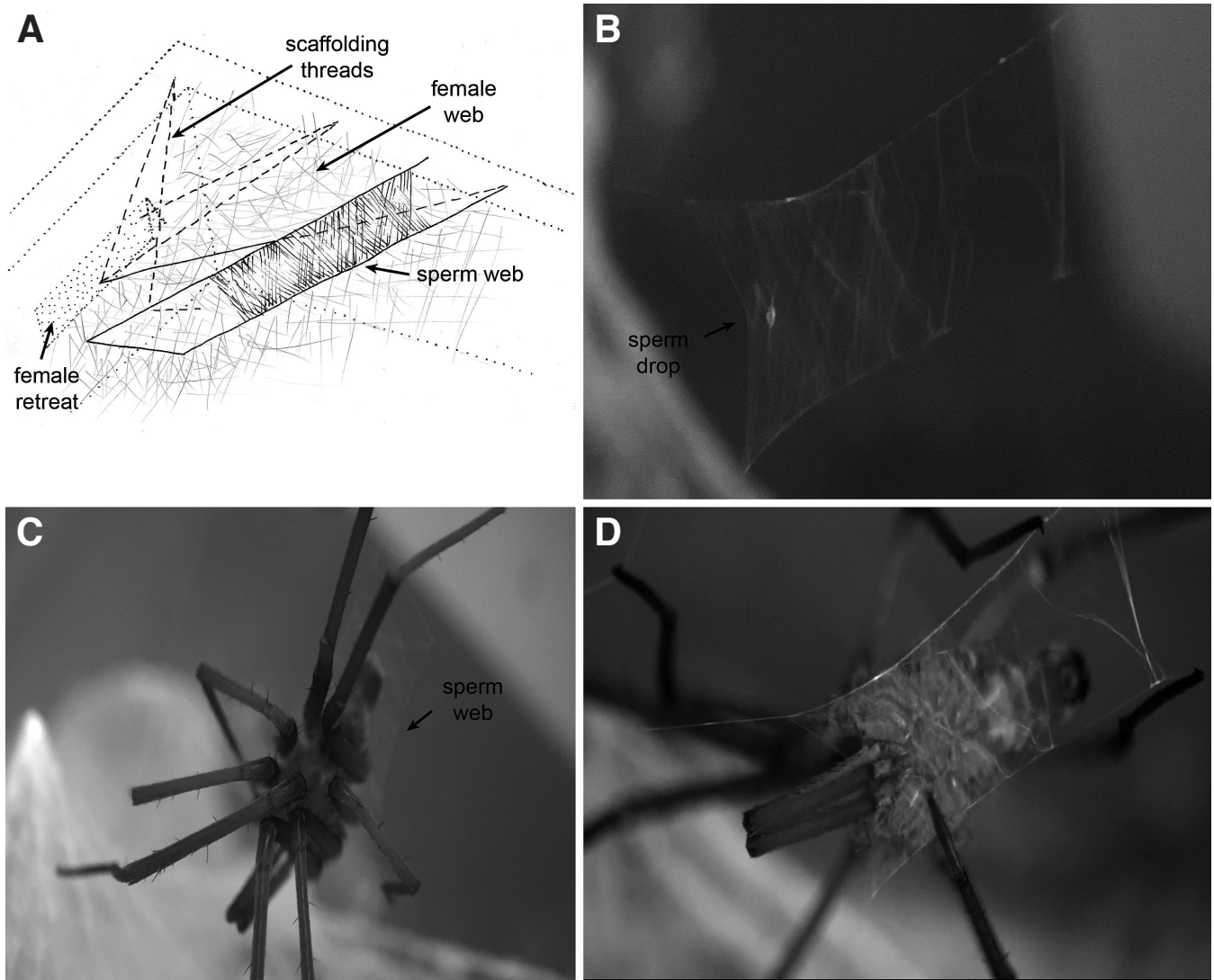


Fig. 3: Sperm web and male behaviour during sperm induction. **A** Scaffolding constructed by the male as support for the sperm web; **B** Sperm web with a residual sperm drop; **C** Position of the male's legs as he produces the sperm onto the sperm web; **D** Male inducing sperm into his pedipalps.

often moved his abdomen backwards by bending his legs slightly, and laid a new swath of threads on a section of the sperm web to which threads had previously been attached. When he finished after 1 min 25 s, the sperm web consisted of a dense sheet of silk threads between two parallel threads (Fig. 3B). In all cases in which the male attached one scaffolding thread to another, or the swath of silk to the parallel threads, he grasped one parallel thread with one leg III just anterior to his spinnerets, and then attached the new threads by lowering his spinnerets. The angle of view prevented us from seeing whether the male used his epiandrous glands to add additional silk on the sheet sperm web, but a close examination of the sperm web (using close-up pictures) did not show anything to suggest that.

Once the web was finished, the male placed his left and right legs III and IV on the parallel threads, and the other two right legs on an adjacent thread, such that the tips of all femora were directed dorsally and nearly perpendicular to his longitudinal axis (Fig. 3C), and during 3 min 12 s the male jerked 1.5 times/s (89 times in one minute recorded), moving all femora towards the centre of the carapace and raising his abdomen with each jerk. His pedipalps also moved during this period, but not with the same rhythm, and

often they contacted his mouthparts. He then moved under the web, leaving a large, whitish drop of semen on top of the web. The male reached around from under the web to place the tips of his pedipalps into the semen drop and, after 7 min 15 s he withdrew most, but not all, of the semen (Figs. 3B, D). During sperm induction, the male's pedipalps moved with a low amplitude but extremely fast vibratory movement. The male then placed his pedipalps in his mouthparts and, after a few seconds, he continued courting the female.

Egg sac construction

The two females that were free in a house began egg sac construction within the tunnel retreat. One female began construction within the tunnel during the late afternoon (1630 h), producing first a dense concave sheet on the floor of the tunnel as deep as the height of her cephalothorax (Fig. 4A) and attached to threads of the tunnel wall. For the construction of this dense, concave sheet, she exclusively used her spinnerets, never using her legs IV to manipulate silk. She placed her spinnerets against the threads of the tunnel or on threads of the concave sheet, then raised her

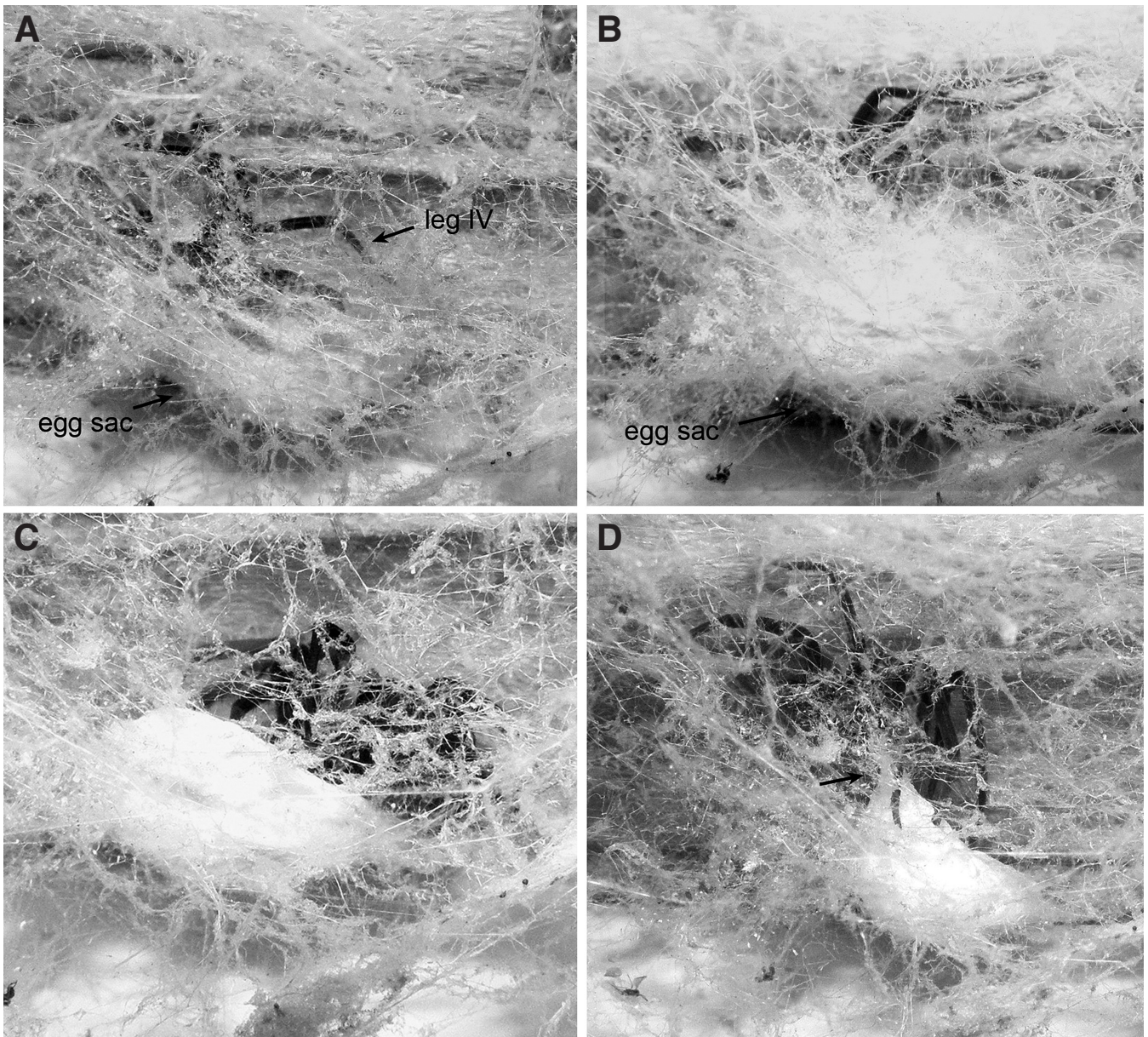


Fig. 4: Different phases of egg sac construction. **A** Construction of a concave platform that constitutes the bottom of the egg sac; **B** Egg sac nearly finished; **C** The female closing the egg sac after laying the eggs; the egg sac has collapsed under the spider's weight; **D** The female pulling the outer layer of the egg sac (black arrow) with her chelicerae after completely closing the egg sac.

abdomen and moved between 1–2 mm, either forwards or towards one side, before touching her spinnerets to the other threads. When her leg I and palps contacted the edge of the concave sheet, she turned approximately 180° and continued adding new threads to the sheet. She then remained resting on it for about four hours (2043 h).

At this point, a male walked into her web, began to court, and copulation occurred. After copulation, the female returned to the partially constructed egg sac and, after some minutes, she resumed its construction. From the border of the concave sheet, she began the construction of a wall that ended with the construction of an empty, nearly ovoid structure that was as tall as the length of her entire body and open at its upper section (Fig. 4B). For its construction, the spider also used only her spinnerets to build the egg sac, and remained inside it during the entire construction sequence. Sometimes her spinnerets were visible at the edge of the empty egg sac, while at other times her legs I and palps were

seen, indicating that the spider had turned inside the egg sac while laying threads. The spider ended the construction of the egg sac at 0048 h (the next day), and remained there for nearly 11 h until she laid her eggs. It was possible to see the mass of eggs deposited at the bottom of the egg sac and the diffuse shape of the spider's body through the egg sac wall.

About 15 minutes after laying the eggs, the spider emerged from the egg sac and began to close the upper opening, an activity that lasted more than three hours (1130–1408 h). She closed the opening with silk, using only her spinnerets, and paused often to pull the edges of the opening together using her chelicerae and pedipalps. Laying threads and pulling the edges alternated during the first hour of closing; afterwards she stopped pulling the edges but continued applying threads to close the opening. As the spider continued applying threads to the opening, the ovoid egg sac collapsed gradually, under the weight of the spider, to about a quarter of the original volume (Fig. 4C).

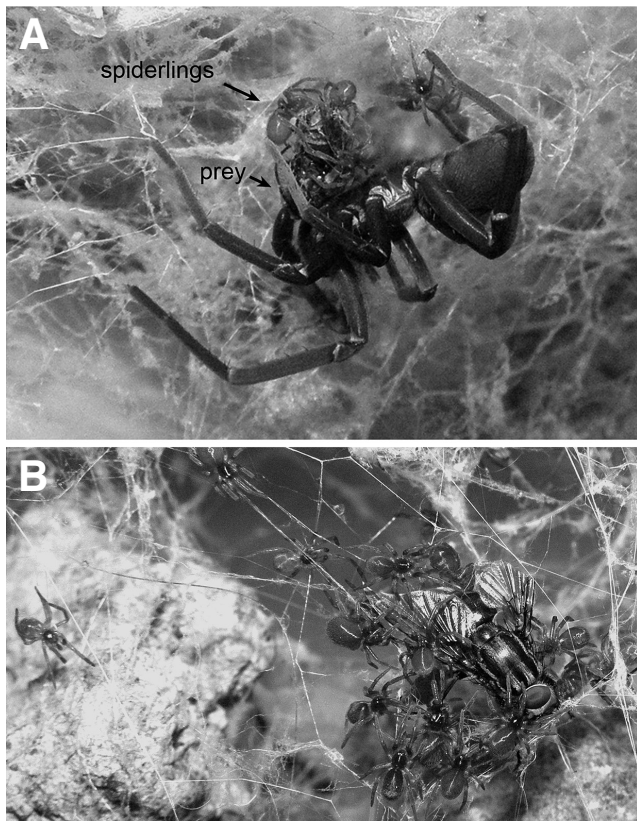


Fig. 5: First instar spiderlings feeding outside the egg sac. **A** Spiderlings and adult female feeding on the same prey; **B** Spiderlings feeding on a flesh fly after a cooperative attack.

After pausing for more than an hour, the spider began pulling the wall of the upper, flat side of the egg sac (the last section to be closed) (Fig. 4D), and cutting the threads that connected the egg sac with the threads of the tunnel. She used her pedipalps apparently to find the threads, and her chelicerae to cut them; on several occasions we saw the spider pulling and breaking the threads with her chelicerae. This activity lasted for nearly three hours, until the egg sac became ovoid again. The spider did not apply threads to the egg sac during this time. The next day the spider moved the egg sac deeper inside the tunnel, where she applied cribellate threads to the outer surface of the egg sac. The egg sac construction behaviour of a second female was very similar, but we did not record the time spent in each phase.

Maternal care and the cooperative behaviour of spiderlings

All females that copulated during the study period produced fertile eggs. Spiderlings emerged from all of them after 80 ± 2.8 days ($n = 2$ egg sacs) at an average ambient temperature of $18 \pm 3^\circ\text{C}$. In all cases, the females cared for the spiderlings that remained in her web until they reached the second, and sometimes the third, instar after emerging from the egg sac. During this time, the female killed prey and allowed spiderlings to feed on it (Fig. 5A). Three females killed prey and carried it inside the tunnel where spiderlings were resting, and left it there for them to feed upon. Often the adult female fed for a few minutes on the

prey she had just killed and then left it for the spiderlings, who continued feeding for hours.

Spiderlings cooperated in killing large prey. Soon after we offered spiderlings a house fly or a flesh fly (an estimated 10 times the weight of a spiderling), they approached it and the one that arrived first nearly always bit and pulled a leg or wing, the next did the same, and the rest (sometimes up to 10 spiderlings) bit different parts of the body (Fig. 5B). Movements of the fly ceased after a few minutes and spiderlings continued feeding on the prey.

Misionella mendensis

Courtship behaviour

The courtship behaviour of *M. mendensis* differed in some respects from that of *K. hibernalis*. We did not see the male adding threads or hooking claws, but we did see mutual male–female tapping with their legs during courtship. In addition, the male rubbed (or at least contacted) the trochanter–femur III of the female with his tarsus II (Fig. 6A–B). In the partial courtship sequence observed, the male used the modified metatarsi–tarsi on his legs II (Ramírez & Grismado 1997; Fig. 6C) to lock them onto the female's femur II, with the tip of his tarsus II resting on her trochanter–femur III. After a few moments, the couple disengaged without initiating copulation, possibly disturbed by the camera's flash.

Discussion

Several features of the courtship behaviour of *K. hibernalis* are apparently unique, some are shared with other members of the family, and still other features are also present in related and unrelated groups. For instance, adding threads to the female web is a behaviour that has not been observed in other filistatids, nor has it been described (to our knowledge) in other spiders. Considering the time the male spends adding threads and the large amount of silk involved, the cost for the male must be high. It is possible that the threads the male adds are impregnated with a pheromone that serves as a chemical signal, and constitutes part of a multimodal signal to courting the female as in other families (Uhl & Elias 2011). Sex pheromones are produced by receptive females of many different families (Foelix 2011) and by males in some lycosids with reversed sexual roles (Aisenberg & Costa 2008; Aisenberg *et al.*, 2008, Aisenberg, Baruffaldi & González 2010). In the case of *K. hibernalis*, the pheromones produced by the male may have a different role (e.g. reducing female aggressiveness), but experimental and anatomical research is needed to test this hypothesis. Similarly, hooking claws and the prenuptial dance are apparently also unique features in the courtship behaviour of *K. hibernalis*, since similar behaviours have not been observed in other filistatids or in other spiders. The prenuptial dance, which is only possible after hooking claws, may serve for the female to evaluate the size or strength of the male.

The rubbing by the male with his legs III was highly stereotyped in *K. hibernalis*, both in the sequence of

events, and in the specific, symmetric position of legs III, widely open in an unusual angle. Fragmentary observations from the small filistatid spider *M. mendensis* suggest that the stereotyped rubbing behaviour may be widespread in the family Filistatidae, but with notable variations. In *M. mendensis*, the male used his legs II, rather than legs III as in *K. hibernalis*, to contact the basal segments of the female's leg II. In *M. mendensis*, as well as in species of the closely related genus *Pikelinia*, the ectal side of the metatarsi and tarsi of leg II are modified in a clasping structure, with several macrosetae associated with a depressed area (Ramírez & Grismado 1997; Fig. 6C). In the partial courtship sequence observed in *M. mendensis*, the male used the claspers on his legs II to lock onto the female's femur II. This occurred without locking of the claws. The family Filistatidae is currently divided in two main clades: Filistatinae and Prithinae (Gray 1995; Ramírez & Grismado 1997). *Kukulcania hibernalis* and *M. mendensis* are representatives of the former and latter subfamilies, respectively. Given that both seem to use a stereotyped rubbing on the female legs II and III during courtship, rubbing, with either male leg II or III may be common to the whole family.

On the contrary, male abdomen vibration (percussion) is a common feature of the courtship behaviour of many araneomorph spiders that have sheet webs or that court directly on the ground, where acoustic signals are transmitted efficiently (Uetz & Stratton 1982). The information transmitted by acoustic waves could inform the female of the male quality (e.g. size) and/or could reduce her aggressiveness. In theraphosids, abdomen vibration seems to be absent, but similar behaviours which may be homologous, such as body vibration (Costa & Pérez-Miles 2002) and body shaking (Yáñez, Loch & Macías-Ordóñez 1999) occur. Both adding threads on the female web and male abdomen vibration seem to reduce female aggressiveness, and could also induce her to cooperate and use the male's sperm to fertilize her eggs (Eberhard 1996; Stratton *et al.* 1996; Eberhard & Huber 1998; Peretti, Eberhard & Briceño 2006; Barrantes 2008).

The copulation position of *K. hibernalis* and *M. mendensis* is similar in some respects to that of theraphosids. In both filistatids and theraphosids the male faces the female and holds her legs (and fangs in theraphosids), and using his legs the male holds her back, raising her, as she lifts her cephalothorax backwards (Yáñez, Loch & Macías-Ordóñez 1999; Costa & Pérez-Miles 2002; Bertani, Fukushima & da Silva Júnior 2008). A similar behaviour was also described for *Hickmania troglodytes* (Doran, Richardson & Swain 2001), a Tasmanian spider of the family Austrochilidae, another basal araneomorph (Coddington 2005).

The sperm web constructed by the male *K. hibernalis* differs in most respects from those described for other araneomorph spiders (Foelix 2011), but shares some general features with sperm webs of theraphosids (Costa & Pérez-Miles 2002). The male *K. hibernalis* constructs a large sperm web apparently exclusively using threads from his spinnerets, rather than using silk from his epiandrous glands to spin the sperm web, as in most araneomorph spiders (Peters & Kooor 1991), even though the males have well developed epiandrous spigots (Griswold *et al.* 2005). The sperm web of *K. hibernalis* resembles those of theraphosids that

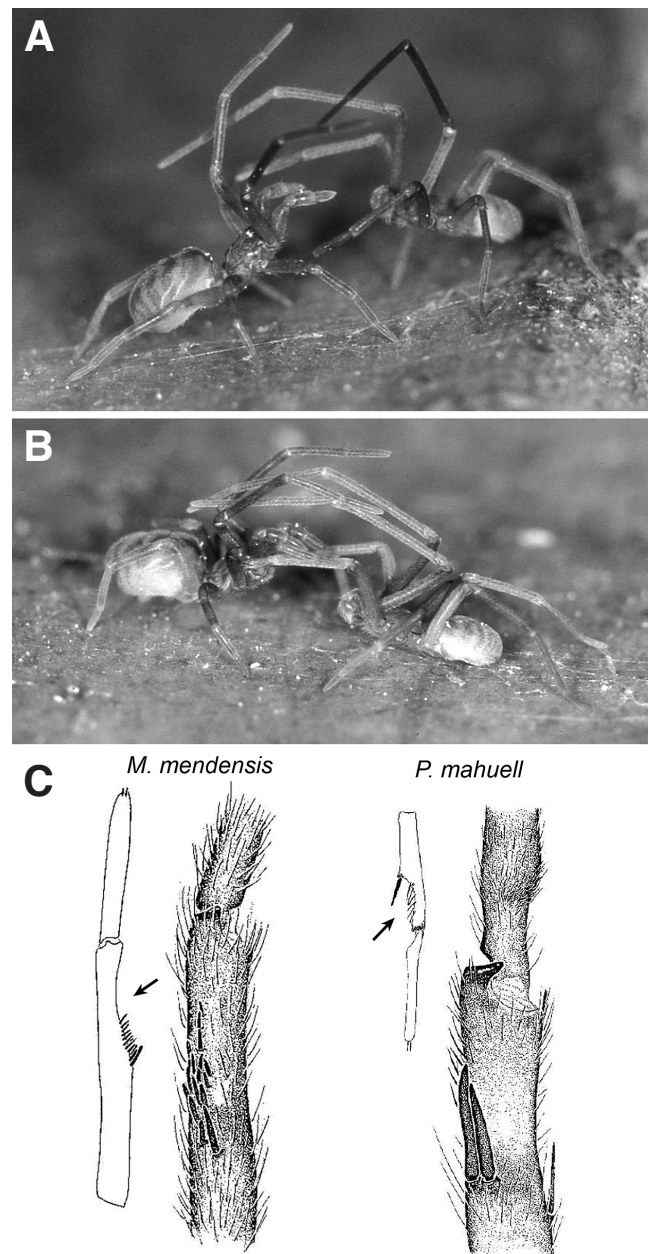


Fig. 6: A, B: Courtship of *Misionella mendensis*; C: leg modifications of *M. mendensis* and *Pikelinia mahuell*. **A** The male starts sliding his leg II on the female femur II; **B** The male is clasping the female femur II using his modified metatarsus and tarsus; **C** Modification of femur II in *M. mendensis* and *P. mahuell*.

construct a large sperm web sheet using silk from the spinnerets, in which males reinforce a small area (where sperm will be deposited), apparently with epiandrous silk (Costa & Pérez-Miles 2002). Thus, the sperm web of *K. hibernalis* seems to be more similar to the web of theraphosids than to the sperm web of other araneomorphs.

Maternal care in *K. hibernalis* includes several aspects. A female lays cribellate silk on the outside of the egg sac, which is maintained deep inside the tunnel retreat, and she guards it there until the spiderlings emerge (Curtis & Carrel 1999). Females of *Thaida peculiaris*, another member of Austrochilidae (Lopardo *et al.* 2004), and female *Zosis geniculata* (GB unpublished data) in the distant family Uloboridae also add cribellate silk to the external layer of the egg sac. This cribellate silk layer likely protects eggs against egg parasites (e.g. *Baeus* wasps) and some predators.

After emerging, the female often provides her offspring with prey, as reported by Curtis & Carrel (1999) for this species, and by Cokendolpher & MacDonald (2007) for *K. geophila*. The cooperative attack of spiderlings against large prey, also seen in *K. geophila* (Cokendolpher & MacDonald 2007), confirms some degree of sociality (subsociability) in the genus *Kukulcania*.

Some behaviours of *K. hibernalis* (e.g. copulation position, sperm web) are more similar to those of theraphosids than to araneomorphs, thus supporting the hypothesis that Filistatidae should have a more basal phylogenetic position within Araneomorphae (Lopardo *et al.* 2004; Griswold *et al.* 2005; Ramírez & Grismado 2008).

Acknowledgments

We thank W. G. Eberhard and two anonymous reviewers for providing valuable comments that greatly improved this manuscript. Research by GB was supported by the Vicerrectoría de Investigación, Universidad de Costa Rica.

References

- AISENBERG, A. & BARRANTES, G. 2011: Sexual behavior, cannibalism, and mating plugs as sticky traps in the orb weaver spider *Leucauge argyra* (Tetragnathidae). *Naturwissenschaften* **98**: 605–613.
- AISENBERG, A. & COSTA, F. 2008: Reproductive isolation and sex-role reversal in two sympatric sand-dwelling wolf spiders of the genus *Allocosa*. *Canadian Journal of Zoology* **86**: 648.
- AISENBERG, A., BARUFFALDI, L. & GONZÁLEZ, M. 2010: Behavioral evidence of male volatile pheromones in the sex-role reversed wolf spiders *Allocosa brasiliensis* and *Allocosa alticeps*. *Naturwissenschaften* **97**: 63–70.
- AISENBERG, A., ESTRAMIL, N., GONZÁLEZ, M., TOSCAZOGA, C. A. & COSTA, F. 2008: Silk release by copulating *Schizocosa malitiosa* males (Araneae, Lycosidae): a bridal veil? *Journal of Arachnology* **36**: 204–206.
- BARRANTES, G. 2008: Courtship behavior and copulation in *Tengella radiata* (Araneae, Tenggellidae). *Journal of Arachnology* **36**: 606–608.
- BARRANTES, G. & EBERHARD, W. G. 2007: The evolution of prey wrapping behavior in spiders. *Journal of Natural History* **41**: 1631–1658.
- BERTANI, R., FUKUSHIMA, C. S. & DA SILVA JÚNIOR, P. I. 2008: Mating behavior of *Sickius longibulbi* (Araneae, Theraphosidae, Ischnocolinae), a spider that lacks spermathecae. *Journal of Arachnology* **36**: 331–335.
- CHAMBERLIN, R. V. & IVIE, W. 1935: Miscellaneous new American spiders. *Bulletin of the University of Utah* **26**(4): 1–79.
- CODDINGTON, J. A. 2005: Phylogeny and classification of spiders. In D. Ubick, P. Paquin, P. E. Cushing & V. Roth (eds.), *Spiders of North America: an identification manual*. College Park, MD: American Arachnological Society: 18–24.
- COKENDOLPHER, J. C. & MACDONALD, K. 2007: Egg guarding and spiderling group-feeding in crevice weaver spiders (Araneae: Filistatidae). *Revista Ibérica de Aracnología* **16**: 67–70.
- COSTA, F. G. & PÉREZ-MILES, F. 2002: Reproductive biology of Uruguayan theraphosids (Araneae, Mygalomorphae). *Journal of Arachnology* **30**: 571–587.
- CURTIS, J. T. & CARREL, J. E. 1999: Social behaviour by captive juvenile *Kukulcania hibernalis* (Araneae: Filistatidae). *Bulletin of the British Arachnological Society* **11**: 241–246.
- DORAN, N. E., RICHARDSON, A. M. M. & SWAIN, R. 2001: The reproductive behaviour of the Tasmanian cave spider *Hickmania troglodytes* (Araneae, Austrochilidae). *Journal of Zoology* **253**: 405–418.
- EBERHARD, W. G. 1996: *Female control: sexual selection by cryptic female choice*. Princeton, New Jersey: Princeton University Press.
- EBERHARD, W. G. & HUBER, B. A. 1998: Courtship, copulation and sperm transfer in *Leucauge mariana* (Araneae, Tetragnathidae) with implications for higher classification. *Journal of Arachnology* **26**: 342–368.
- FOELIX, R. F. 2011: *Biology of spiders*. Oxford & New York: Oxford University Press.
- GERTSCH, W. J. 1949: *American spiders*. Princeton, New Jersey: Van Nostrand.
- GRAY, M. R. 1995: Morphology and relationships within the spider family Filistatidae (Araneae: Araneomorphae). *Records of the Western Australian Museum, Supplement* **52**: 79–89.
- GRISWOLD, C. E., RAMÍREZ, M. J., CODDINGTON, J. A. & PLATNICK, N. I. 2005: Atlas of phylogenetic data for entelegyne spiders (Araneae, Araneomorphae, Entelegynae), with comments on their phylogeny. *Proceedings of the California Academy of Sciences, 4th. Series* **56** Supplement II: 1–324.
- HEBETS, E. A. & UETZ, G. W. 2000: Leg ornamentation and the efficacy of courtship display in four species of wolf spider (Araneae: Lycosidae). *Behavioral Ecology and Sociobiology* **47**: 280–286.
- HENTZ, N. M. 1842: Descriptions and figures of the araneides of the United States. *Boston Journal of Natural History* **4**: 54–57, 223–231, pl. 8.
- KNOFLACH, B. 2004: Diversity in the copulatory behaviour of comb-footed spiders (Araneae: Theridiidae). *Denisia* **12**: 161–256.
- LOPARDO, L., RAMÍREZ, M. J., GRISMADO, C. & COMPAGNUCCI, L. A. 2004: Web building behavior and the phylogeny of austrochiline spiders. *Journal of Arachnology* **32**: 42–54.
- MELLO-LEITÃO, C. F. de 1920: Algumas aranhas novas. *Revista Sociedade Brasileira de Ciência* **3**: 169–176.
- PERETTI, A., EBERHARD, W. G. & BRICEÑO, R. D. 2006: Copulatory dialogue: females sing during copulation to influence male genitalic movements. *Animal Behaviour* **72**: 413–421.
- PETERS, H. M. & KOVOOR, J. 1991: The silk-producing system of *Linyphia triangularis* (Araneae, Linyphiidae) and some comparisons with Araneidae. *Zoomorphology* **111**: 1–17.
- PLATNICK, N. I., CODDINGTON, J. A., FORSTER, R. R. & GRISWOLD, C. E. 1991: Spinneret morphology and the phylogeny of haplogyne spiders (Araneae, Araneomorphae). *American Museum Novitates* **3016**: 1–73.
- RAMÍREZ, M. J. 2000: Respiratory system morphology and the phylogeny of haplogyne spiders (Araneae, Araneomorphae). *Journal of Arachnology* **28**: 149–157.
- RAMÍREZ, M. J. & GRISMADO, C. J. 1997: A review of the spider family Filistatidae in Argentina (Arachnida, Araneae), with a cladistic reanalysis of filistatid genera. *Entomologica Scandinavica* **28**: 319–349.
- RAMÍREZ, M. J. & GRISMADO, C. J. 2008: Filistatidae. In L. E. Claps, G. Debandi & S. Roig-Juñent, (eds.), *Biodiversidad de artrópodos Argentinos, Vol. 2*. Mendoza: Editorial Sociedad Entomológica Argentina: 79–83.
- ROBINSON, M. H. & ROBINSON, B. 1980: Comparative studies of the courtship and mating behavior of tropical araneid spiders. *Pacific Insects Monograph* **36**: 1–218.
- SCHNEIDER, J. & ANDRADE, M. 2011: Mating behaviour and sexual selection. In M. E. Herberstein (ed.), *Spider behaviour. flexibility and versatility*. Cambridge & New York: Cambridge University Press: 215–274.
- STRATTON, G. E., HEBETS, E. A., MILLER, P. R. & MILLER, G. L. 1996: Pattern and duration of copulation in wolf spiders (Araneae, Lycosidae). *Journal of Arachnology* **24**: 186–200.
- UETZ, G. W. & STRATTON, G. E. 1982: Acoustic communication and reproductive isolation in spiders. In P. N. Witt & J. S. Rovner (eds.), *Spider communication. Mechanisms and ecological significance*. Princeton, New Jersey: Princeton University Press: 123–159.
- UHL, G. & ELIAS, D. O. 2011: Communication. In M. E. Herberstein (ed.), *Spider behaviour. flexibility and versatility*. Cambridge & New York: Cambridge University Press: 125–189.
- UHL, G., SCHMITT, S. & SHÄFER, M. 2005: Fitness benefits of multiple mating versus female mate choice in the cellar spider (*Pholcus phalangioides*). *Behavioral Ecology and Sociobiology* **59**: 69–76.
- YÁÑEZ, M., LOCHT, A. & MACÍAS-ORDÓÑEZ, R. 1999: Courtship and mating behavior of *Brachypelma klaasi* (Araneae, Theraphosidae). *Journal of Arachnology* **27**: 165–170.