# Behavioral roles of the sexually dimorphic structures in the male harvestman, *Phalangium opilio* (Opiliones, Phalangiidae)

**Rodrigo H. Willemart, Jean-Pierre Farine, Alfredo V. Peretti, and Pedro Gnaspini**

**Abstract:** In various animal species, male sexual dimorphic characters may be used during intrasexual contests as ornaments to attract females, or to hold them before, during, or after copulation. In the well-known harvestman, *Phalangium opilio* L., 1758, the behavioral functions of these male sexually dimorphic structures have never been studied in detail. Therefore, in addition to a morphometric study, 21 male contests and 43 sexual interactions were analyzed. Our observations revealed that during contests, the male cheliceral horns form a surface by which the contestants use to push each other face-to-face while rapidly tapping their long pedipalps against the pedipalps of the opponent, occasionally twisting the opponent's pedipalp. Scanning electron micrographs revealed contact mechanoreceptors on the pedipalp that would detect the intensity–frequency of contact with the contender's pedipalp. Larger males won almost all contests, whereas the loser rapidly fled. During sexual interactions, the longer pedipalps of the male held legs IV of the female, whereas males with shorter pedipalps held the female by legs III. No contact with the male pedipalps and chelicerae by the females was visible before, during, or after copulation. Soon after copulating, males typically bent over the female, positioning their cheliceral horns against the females's dorsum. Consequently, our data show that the cheliceral horns and the longer pedipalps of the male seem to play an important role, during both intersexual and intrasexual encountering.

**Résumé :** Chez de nombreuses espèces animales, les ornementations sexuellement dimorphiques des mâles peuvent être utilisées lors des combats rituels entre mâles ou comme signal afin d'attirer les femelles ou les retenir avant, pendant et après l'accouplement. Chez l'opilion *Phalangium opilio* L., 1758, le rôle précis joué par ces structures n'a jamais été mis en évidence. Au cours de ce travail, outre une étude morphométrique, nous avons analysé, grâce à des enregistrements vidéo, 21 combats entre mâles et 43 accouplements. Nous avons pu montrer que, lors des combats, les mâles utilisent les cornes portées par les chélicères pour se repousser lorsqu'ils sont face-à-face, tout en se tapant mutuellement à l'aide de leurs longs pédipalpes, voire en les enroulant avec ceux de l'adversaire. Des micrographies réalisées au microscope électronique à balayage révèlent l'existence de mécanorécepteurs sur les pédipalpes qui pourraient permettre au mâle de détecter la fréquence et l'intensité des contacts des pédipalpes de son adversaire. Les mâles les plus grands gagnent presque tous les combats, le perdant fuyant rapidement. Au cours du comportement sexuel, les mâles à grands pédipalpes les utilisent pour agripper les pattes IV de la femelle, alors que les mâles à pédipalpes plus courts les retiennent par les pattes III. Il n'y a aucun contact tactile de la part des femelles avec les pédipalpes et les chélicères des mâles avant, pendant et après l'accouplement. Juste après l'accouplement, le mâle s'appuie sur le dos de la femelle à l'aide des cornes de ses chélicères. D'après nos observations, il semble donc que les chélicères et les longs pédipalpes des mâles jouent un rôle non négligeable lors des interactions intra- et inter-sexuelles chez cette espèce.

## Introduction

Sexually dimorphic structures are found throughout the animal kingdom, occurring among several arthropods, amphibians, reptiles, mammals, and birds (Darwin 1871). These structures are usually conspicuously different in males and may be sexually selected, being used by females in mate choice, in contests with other males, and (or) to help males hold females to mate (Andersson 1994).

Among arthropods, to mention a few examples, chelae in crabs (Sneddon et al. 1997) and pseudoscorpions (Zeh 1987) and mandibles in orthopterans (Bateman 2000) are sexually dimorphic and used in male–male contests. Perhaps one of the most studied cases of sexual dimorphism related to male–male contests is that of beetles (Eberhard 1982; Cook 1990). In several species, males have horns used to displace the rival by pushing it, prying it away from the substrate, or dropping it from a stem (Eberhard 1979, 1980). Larger

males with larger horns win most contests (Moczek and Emlen 2000; Emlen 2001).

Sexual dimorphisms can also be used in intersexual interactions, influencing females in mate choice. Displays that involve exhibiting tufts of setae in some male spiders (Hebets 2004) and the wing color pattern in some male dragonflies (Moore 1990) are examples of arthropod characteristics used by females to choose a mate. These are displays used in visual animals, but vibratory, tactile, or chemical stimulation do occur not only among nonvisual but also among visual species (Mora 1990; Candolin 2003; Hebets and Papaj 2005).

Males of some arthropod species use sexually dimorphic structures to maintain a tight grip on females during copulation (Eberhard 1996), not allowing them to escape or attack the male (Arnqvist 1989; Hume et al. 2005). Therefore, whether sexually dimorphic structures are used for male–male contests, displays, luring of females, forceful copulation, or defence during intercourse, functional explanations can often be obtained by observations made during male–male interactions and sexual behaviors.

The present study focused on this subject, exploring the use and possible function of sexually dimorphic structures in *Phalangium opilio* L., 1758 (Opiliones, Phalangiidae). Savory (1962) wrote that *P. opilio* was "known to Aristotle, mentioned by Robert Hooke, named by Linnaeus and recognizably illustrated by many medieval naturalists". The sexually dimorphic chelicerae of *P. opilio* are illustrated in several old European books (de Graaf 1882; Claus and Moquin Tandon 1884; Lennis 1886). Researchers also noted the long pedipalps of males (Perrier 1929), which "look like legs" (Stanek 1964), and Planet (1905) reported the great variation in the size of pedipalps and chelicerae of males. Despite being well known and the large number of studies conducted on this species, there have been no functional explanations for their sexual dimorphism. de Graaf (1882) briefly described the mating posture but did not mention any role by the male pedipalps and cheliceral horns. Kästner (1928) only mentioned that males touch their cheliceral horns during contests, with no further comments.

*Phalangium opilio* has a widespread distribution, occurring both in Europe and North America. It can be found on low vegetation and trees, cultivated crops, lawns, gardens, deteriorating buildings, or along roadsides (Clingenpeel and Edgar 1966; Edgar 1990). They have diurnal and nocturnal habits (Kästner 1931; Williams 1962; Edgar and Yuan 1968) and are opportunistic feeders (Bristowe 1949; Butcher et al. 1988; Morse 2001), being relatively abundant in cultivated crops (Juen and Traugott 2004; Allard and Yeargan 2005).

There is no evidence of any difference in microhabitats, feeding, or defensive behavior between males and females, which could explain why males would bear horns on the chelicerae and have longer pedipalps (see discussion in Shine 1989). We therefore raised two nonexclusive hypotheses independently for chelicerae and pedipalps to explain this dimorphism. Hypothesis 1 is that the male cheliceral horns and (or) the longer pedipalps are used in intrasexual interactions. Hypothesis 2 is that these structures are used in intersexual interactions.

## Materials and methods

### Collection and maintenance in captivity

We collected the individuals as adults from August to October 2004 in the Parc de la Collombière in the city of Dijon, Bourgogne State, France, from 1400 to 1800. We found the animals stationary or wandering on leaves of small plants (<0.5 m height) surrounding tree trunks or on the tree trunks from the substrate up to 2 m high. In the laboratory, males were separated from females, and the individuals were maintained together in terraria of 20 cm (height) × 20 cm × 40 cm. These had a loose soil substrate and corks, sticks, and pieces of cardboard to provide shelter and increase the surface area on which the animals could wander and rest. A soaked cotton ball in a Petri dish provided distilled water to the animals. Up to 10 individuals of the same sex were kept in the same terrarium. Other animals were maintained individually in containers of 5 cm (height) × 5 cm × 8 cm with a soil substrate and a soaked cotton ball. All the individuals were kept under a natural light cycle at room temperature (~25 °C), and humidity inside the terraria was not controlled. The animals were fed on macerated cockroaches (*Periplaneta americana* (L., 1758)), pieces of larval *Tenebrio* sp., soaked sweet bread, and mashed potatoes cooked with sausages.

### Morphological features

A sample of animals, including specimens used for behavioral observations, was measured with the aid of the Leica Qwin Standard version 2.4 software. Chelicerae were measured as a straight line from the upper extremity of the second segment (top of the horn in males) to the insertion of the movable finger of chelicerae. The pedipalps were measured from the base of the femur up to the tarsus tip, not including the claw. Prosoma length was measured from its anterior to its posterior limit, and width was taken from the larger region of the prosoma (Fig. 1).

Scanning electron microscope (SEM) images were used to analyze the sensory structures on chelicerae and pedipalps that could be related to contests and copulation. For SEM preparation, the material was submersed in acetone for 3 min and then mounted on an aluminum stub using double stick adhesive tape, sputter-coated with gold, and photographed with a Phillips XL 30 SEM.

### Behavioral observations, intrasexual interactions

Observations of male–male contests were digitally recorded either opportunistically in the collective terraria (*n* = 7) or on testing arenas (*n* = 13) in which both animals were serially introduced 10 cm from one another. This was to avoid a possible effect of asymmetrical territoriality based on the time spent on the arena (Macías-Ordóñez 1997). The arena was either a cork platform (10 cm × 15 cm) on a nonenclosed table or a terrarium (20 cm (height) × 20 cm × 40 cm) with soil and cork as a substrate. The arenas received no females prior to the introduction of males, and the latter had no contact with females for more than 5 days before the observations. Though the cork was not cleaned between each trial and the soil was not changed, the individuals did not tap the ground of the arenas with their pedipalps, which is the typical behavior when they detect

**Table 1.** Difference in pedipalps and chelicerae length between *Phalangium opilio* males and females.

| | Male | | | | Female | | | | Statistic | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | SD | Range | $n$ | Mean | SD | Range | $n$ | $U$ | $P$ |
| Chelicerae | 1.82 | 0.47 | 1.21–3.68 | 55 | 1.23 | 0.09 | 1.07–1.38 | 16 | 151.5 | <0.001 |
| Pedipalps | 9.26 | 2.3 | 6.58–18.99 | 55 | 5.57 | 0.29 | 5.14–6.03 | 13 | 91.0 | <0.001 |

chemicals on the substrate (R.H. Willemart, unpublished data). We therefore reject the possibility that previous individuals left chemicals that influenced their behavior.

### Behavioral observations, intersexual interactions

To digitally record copulatory behavior, we introduced one or two males and females in terraria (20 cm (height) × 5 cm × 40 cm) with humid paper towel substrate (changed after each trial). Introducing more than a couple was a way to increase the chances of contact between mates. The first interaction that resulted in copulation was recorded, and in no case did this pair of mates touch the other individuals before initiating their interaction. The observations were done between August and October 2004 from 1100 to 0400, with artificial white light at daytime and red light at night. Forty-four males and 16 females were used to stage and record 20 fights and 41 copulatory behaviors, and therefore some individuals of both sexes were used more than once. Of these 41 records of copulation, it was possible to see the male's penis in 37, but in the remaining four, all behavioral categories displayed both by males and females (see below) were typical of copulation. In 33 cases, we can be sure penetration occurred, and in 8 we assumed it did because of the typical behaviors displayed by the couple. We should mention, however, that the opening guarded by the female's genital operculum is not the primary genital opening. Because the latter is located at the tip of a retracted ovipositor (de Graaf 1882), penetration of the pregenital chamber does not indicate that male has successfully copulated. We could describe details and quantify the time spent during some behavioral categories by the use of the software Nero Showtime, which allowed us to watch the video frame-by-frame relative to time. As we did not have the body measures of the individuals digitally recorded, we identified them a posteriori from the films as large males (LM) or small males (SM) when possible. Voucher specimens are deposited in the Museu de Zoologia da Universidade de São Paulo (MZUSP).

### Statistical analysis

A Student's *t* or Mann–Whitney *U* test (depending on whether the data was parametric or not) was used to compare the measures obtained for males and females and a Kolmogorov–Smirnof (K–S) test was used to test for normality. A Spearman correlation ($r_S$) was used to compare body size and chelicera and pedipalp length. Comparisons of the behaviors displayed by small and large males were done either with a Student's *t* test or Mann–Whitney *U* test or with a $\chi^2$ (though a Fisher's exact test was used when one of the values was less than 5 — see Zar 1999).

## Results

### Sexual dimorphism and male sensory structures

The morphological differences between the pedipalps and

**Fig. 1.** Dorsal view of adult male of *Phalangium opilio*, showing how the measures of body length (vertical bar) and width (horizontal bar) were taken. Scale bar = 1.5 mm.



chelicerae of male and female *P. opilio* are clearly evident (Table 1; Figs. 2, 3, 4). Prosoma length is a measure of overall male size and had a normal distribution (Fig. 5A; K–S distance = 0.083; $P = 0.429$), whereas their chelicerae and pedipalps did not (K–S distance = 0.229 and 0.219, respectively; $P < 0.001$ for each), with a predominance of short sizes and a greater range of values than prosoma length (Figs. 6A, 7A). Body length vs. body width for males and females followed the same pattern, though females were generally larger (Student's *t* test for body length: $t_{[66]} = 5.89$; $P < 0.001$; Fig. 5B). An increase in body size is followed by an increase in the length of chelicerae and pedipalps in males but not in females (body length vs. chelicerae, males: $r_S = 0.592$, $P < 0.001$, $n = 53$; body length vs. pedipalp, males: $r_S = 0.664$, $P < 0.001$, $n = 53$; body length vs. chelicerae, females: $r_S = 0.442$, $P = 0.109$, $n = 14$; body length vs. pedipalps, females: $r_S = 0.314$, $P = 0.264$, $n = 14$; Figs. 6B, 7B). Male pedipalps and chelicerae had mechanoreceptor hairs (sensilla chaetica; Figs. 8, 9).

### Intersexual interactions, precopulatory behavior

Males never overtly detected the females before contact (with either the legs or body of the female) (100% of the cases with precontact phase recorded; $n = 26/26$). In all of these cases, the males remained for several minutes in the arena with the female, moving legs II as close as 0.5 cm from her legs but remaining quiet. After touching the female, males immediately attempted to copulate.

Upon contact, males attempted to face the female and hold her by her articulation of trochanter – femur III or IV using the metatarsus–tarsus articulation of his pedipalps ($n = 26/26$; Fig. 10). The median time elapsed between first con-

**Fig. 2.** Lateral views of male and female *Phalangium opilio*. Arrows show the left pedipalp of the male and the right pedipalp of the female. Note the sexually dimorphic chelicerae between pedipalps and the body. Scale bar = 5 mm.

**Fig. 3.** Female left chelicerae of *Phalangium opilio*, lateral view. **Fig. 4.** Male left chelicera of *P. opilio*, lateral view.
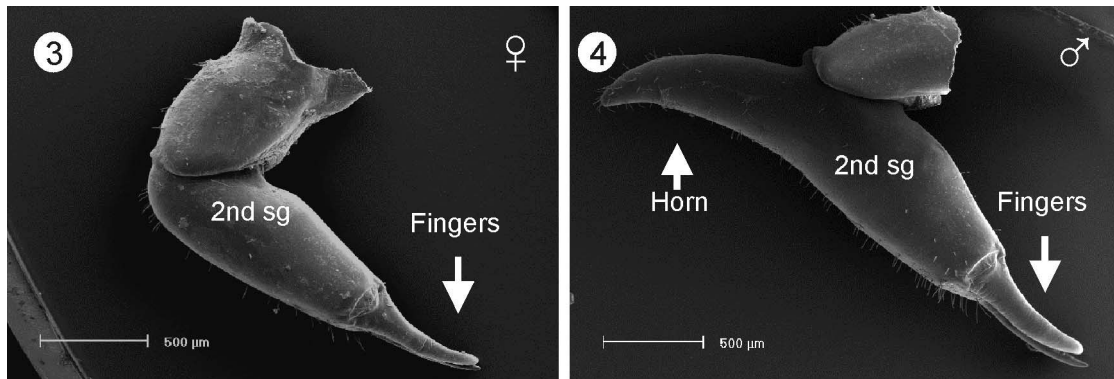
tact and holding the females was 8.5 s (range: 3–25 s, $n$ = 14; no difference between LM and SM: $t$ = 1.074, $P$ = 0.304, $n$ for LM = 6 and $n$ for SM = 8). Simultaneously, males displayed legs I and II agitation, which were very rapid, mainly dorso–ventral movements of legs I and II touching the female ($n$ = 26/26), and cheliceral pinch, in which the male would pinch the dorsum and the proximate regions of female's first cheliceral segment ($n$ = 17; this was 100% of the cases in which it was possible to observe the chelicerae; Fig. 10). Resuming legs I and II agitation, males started displaying leg I stroke, in which they faced the female while holding her and displayed very rapid whipping movements of the tarsus of legs I across her body on the dorsal, lateral, and ventral regions from the posterior region to the chelicerae ($n$ = 25; in one case, the male used legs I to pull the female towards him by her posterior region; Fig. 10).

In some occasions, females displayed vigorous dorso–ventral movements of the body (bouncing) and lowering the prosoma. In two cases, it was possible to observe the male wrapping legs II around a femur of the female when she attempted to flee. Among SM, females displayed bouncing in six cases and remained quiet 11 times, while these numbers for LM were one and six, respectively (LM

vs. SM: Fisher's exact test, $P$ = 0.625). There was no detectable male behavior that elicited female bouncing, no movements of the female, and no specific modification of the male's behavior after the female started to bounce.

Less than a second ($n$ = 13) after facing and holding her, with both sexes approximately in the same plane (longer axis of the body 180° parallel to each other), the male lifted the posterior extremity of his body (~45°–90° in relation to the female; $n$ = 20; this was 100% of the cases in which it was possible to observe it) and extruded his penis. He then lowered this extremity, rubbed the distal portion of the penis shaft between the latero-posterior lobes of the female's mouth ($n$ = 13; this was 100% of the cases in which it was possible to observe if this happened) with back and forward movements of his body (penis rubbing on female's mouth; $n$ = 20; this was 100% of the cases in which it was possible to observe if this happened), and finally inserted it into the pregenital chamber of the female (Fig. 10). Females remained quiet while males displayed penis rubbing on female's mouth ($n$ = 13). Immediately after penetration, females either remained quiet ($n$ = 6) or displayed bouncing ($n$ = 7). There was no difference between LM and SM (Fisher's exact test, $P$ = 1.00). In the four cases in which it was possible to note the exact moment when the shaft was

**Fig. 5.** (A) Histogram of male *Phalangium opilio* body length. (B) Scatterplot of *P. opilio* prosoma length plotted against prosoma width. **Fig. 6.** (A) Histogram of male *Phalangium opilio* chelicera length. (B) Scatter plot of *P. opilio* chelicera length plotted against prosoma length. **Fig. 7.** (A) Histogram of male *P. opilio* pedipalp length. (B) Scatter plot of *P. opilio* pedipalp length plotted against prosoma length. Males are ● and females are ○ in 5B, 6B, and 7B.
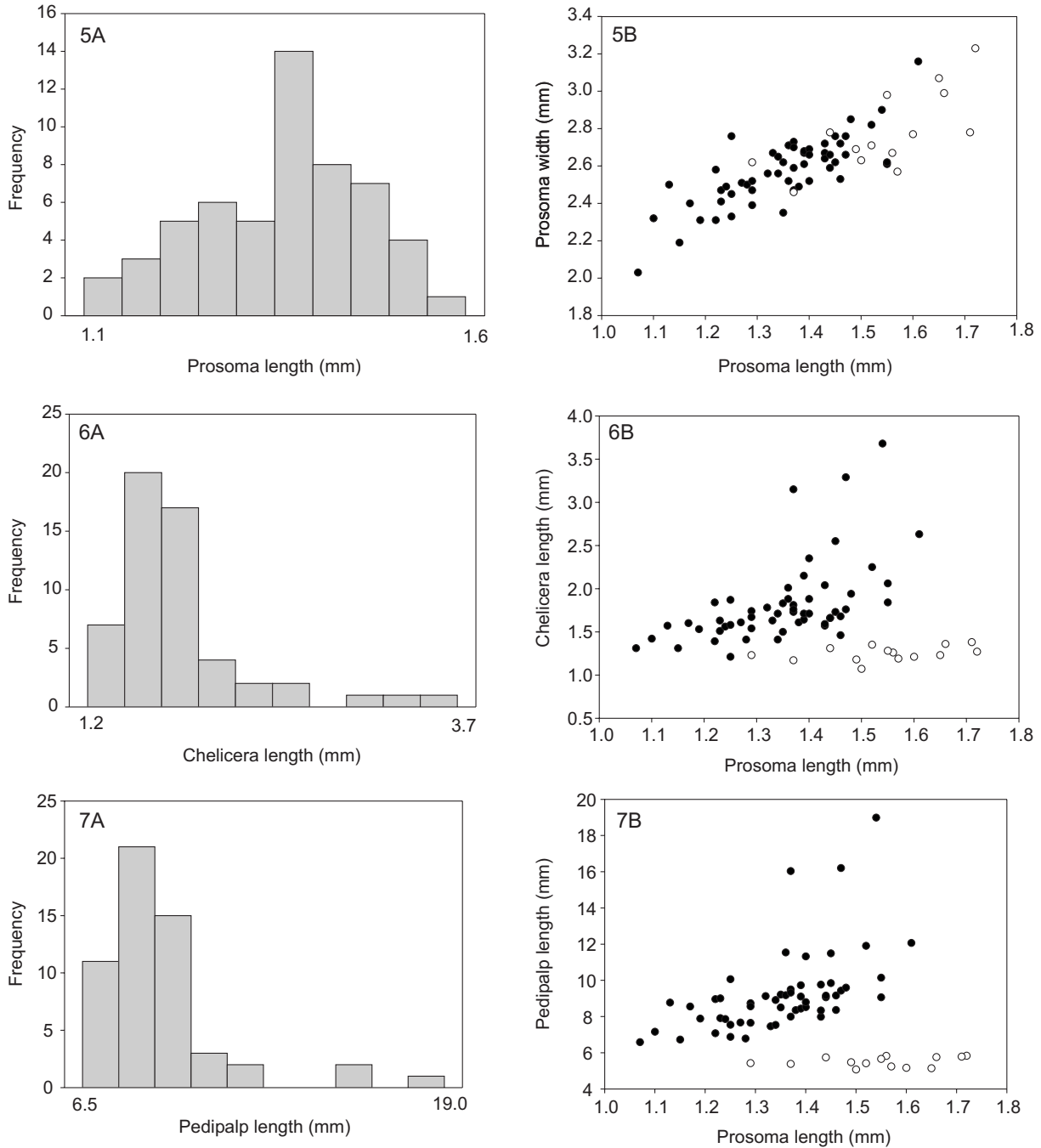
inserted into her pregenital chamber, the males displayed penis rubbing on female's mouth for 3, 3, 4, and 12 s. It was not possible to detect if the female opened her genital operculum or if the male forced the penetration.

**Intersexual interactions, copulatory behavior**

LM used their pedipalps to hold females by legs IV ($n = 12$) or III ($n = 3$) during copulation, whereas SM held females mainly by legs III ($n = 26/26$) and only once by legs IV (LM vs. SM: Fisher's exact test, $P < 0.001$; Figs. 10, 11).

Throughout copulation, males displayed leg I stroke ($n = 41$) and pinched females on the basal segment of their chelicerae or the femur of their pedipalps ($n = 15$; not possible to be sure in the remaining observations). Males also displayed antero-posterior twisting movements, in which the posterior region of his body moved up and down and laterally simultaneously ($n = 25$; in the remaining cases, it was not possible to note the exact movements of the male; Fig. 10). The amplitude of these movements widely varied, sometimes being very evident and in other instances very hard to notice.

**Fig. 8.** Scanning electron micrograph (SEM) showing detail of male *Phalangium opilio* chelicera. All hairs occurring on the chelicerae are of the same type (sensillum chaeticum). **Fig. 9.** SEM showing male *P. opilio* pedipalp, distal portion, lateral view. All hairs inserting at an angle of ~70° to 90° are sensilla chaetica (arrow).
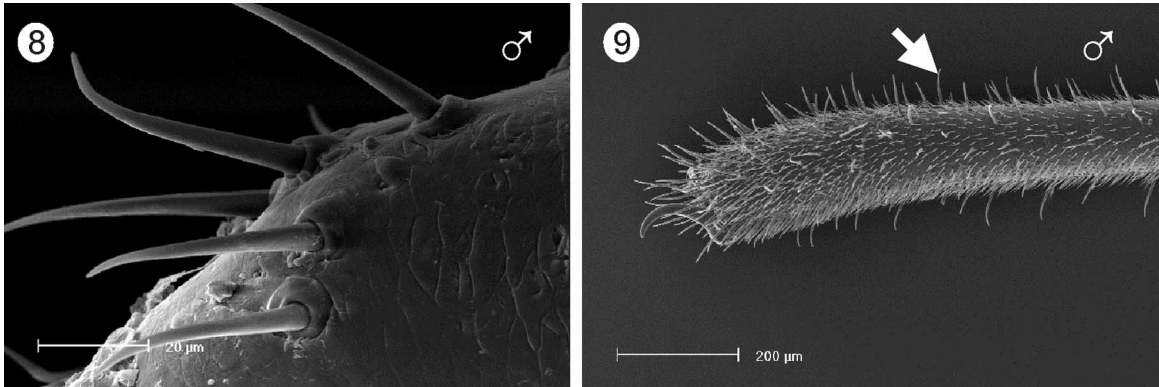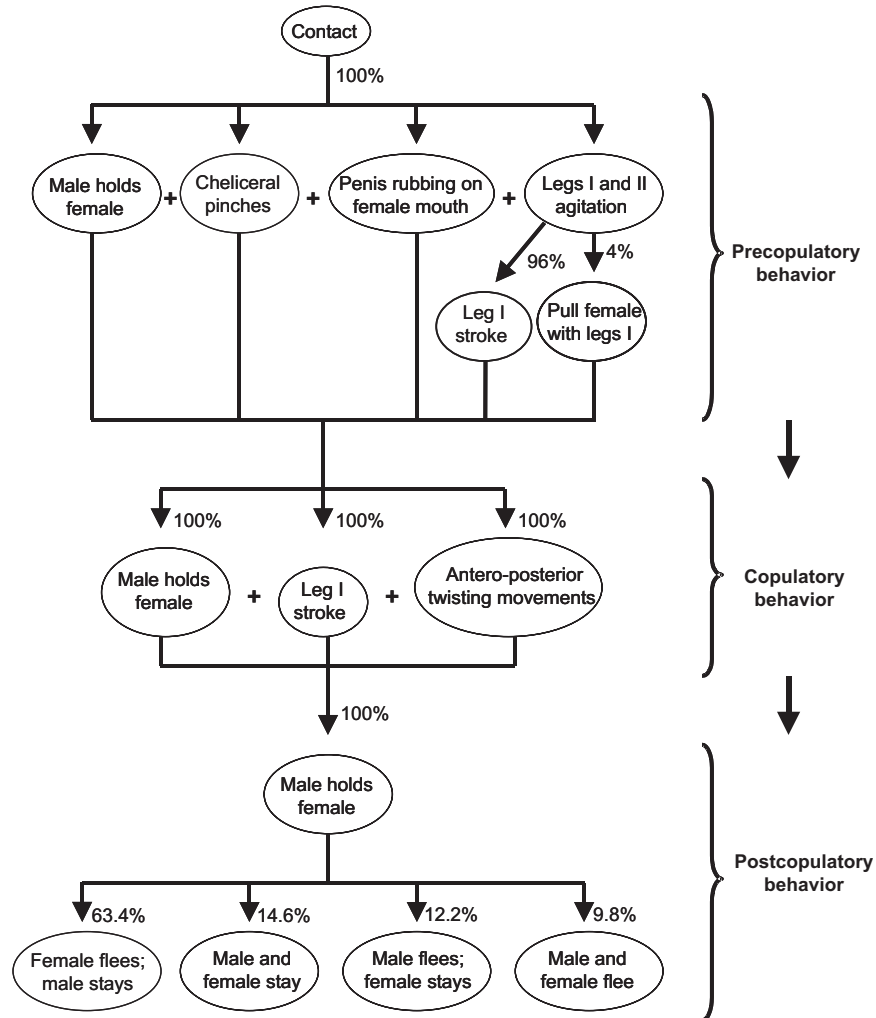


**Fig. 10.** Diagram of male *Phalangium opilio* behaviors that occur before, during, and after copulation.



Females either remained motionless during copulation or displayed bouncing movements, occasionally trying to roll over the male's body, from the anterior to the posterior regions of the male's body. Among SM, females displayed bouncing in 20 cases and remained quiet in seven cases, whereas for LM, these numbers were seven and seven, re-spectively (LM vs. SM: $\chi^2_{[1]} = 0.755$, $P = 0.385$). The female tried to roll over the male in only 1 out of 15 copulations in-volving LM, who could hold her for 7 s before she broke his grip. Females tried to flee by rolling over SM males in 7 out of 28 copulations, and these smaller individuals could hold the females for 10 s (median; range = 4–31 s). Copulation

**Fig. 11.** Male (right) and female (left) of *Phalangium opilio* copulating. White arrow show male's legs during stroke (rapid whipping movements of his tarsus of legs I on her body). Solid arrow points to the metatarsus–tarsus articulation of the male left pedipalp, holding the female by leg IV. Open black arrow on the right shows the penis, with the distal portion inside the female and thus not visible. **Fig. 12.** Male (right) and female (left) of *P. opilio* during postcopulatory behavior. Note the prosoma inclination of the male. Solid arrow points to the metatarsus–tarsus articulation of the male's left pedipalp, holding the female by leg IV. Circle shows the position of male's chelicerae, resting on the female's dorsum. Scale bars = 5 mm.
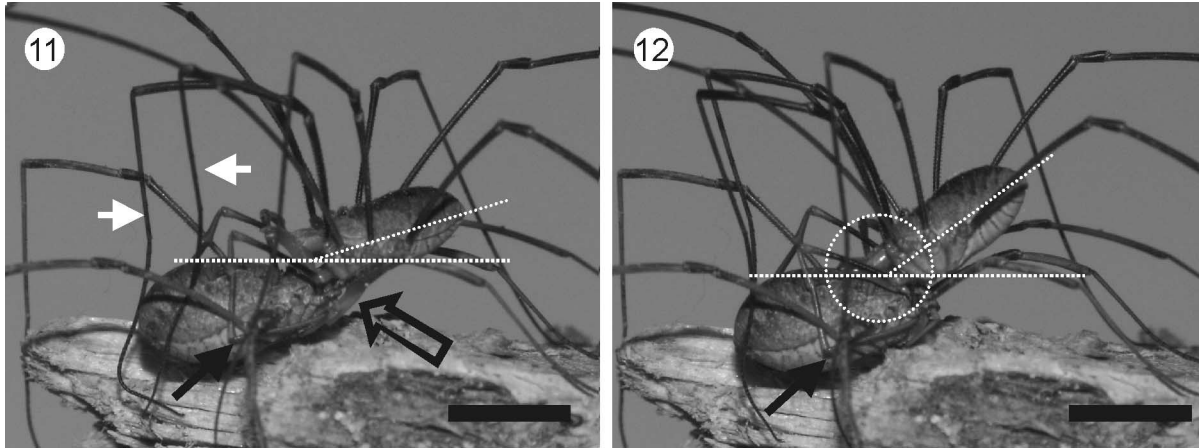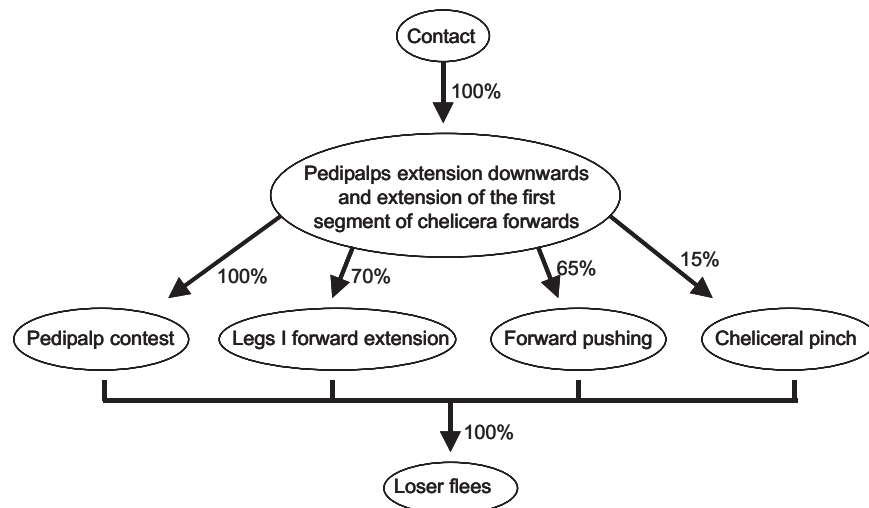


**Fig. 13.** Diagram of male *Phalangium opilio* behaviors during male–male interactions. Percentages do not sum 100% because the behavioral categories occur simultaneously.



duration (penis in – penis out) was 29 s (median; range = 8–88 s, $n = 25$; no difference between LM and SM; $U = 56.5$, $P = 0.181$, $n$ for LM = 6 and $n$ for SM = 19).

**Intersexual interactions, postcopulatory behavior**

In all copulations involving SM, they held the females with their pedipalps ($n = 25$) after copulation ended (Figs. 10, 12). Among LM, 11 held the females and 2 did not (LM vs. SM; Fisher's exact test, $P = 0.111$). When females remained quiet, the male always resumed copulation by maintaining the grip with his pedipalps and retracting his penis from the female's pregenital chamber while displaying prosoma inclination (lifting the posterior region of his body and positioning it to form an angle of ~45° dorsally with the female; $n = 19$; Fig. 12). At that time, females always displayed cheliceral grooming, in which the cheliceral fingers are passed beneath the mouth lobes ($n = 17$: 5 LM and 12 SM; in two cases it was not possible to observe). We cannot

be sure if the males touched the horns of their chelicerae on the dorsum of the female. In this position, males pinched and held females by the basal segment of chelicerae or proximal region of pedipalps ($n = 10$; not possible to observe in the remaining observations). Finally, females broke the grip of males and fled, whereas males did not flee ($n = 26$; LM vs. SM; Fisher's exact test, $P = 1.00$), males fled and females did not ($n = 4$), none of them fled (remaining <1 cm to each other for more than 60 s; $n = 6$), or both fled ($n = 5$). Pooling all data, males spent 14 s holding females after copulation ended (median; range: 0–107 s, $n = 33$; no difference between LM and SM; $U = 192.0$, $P = 0.294$, $n$ for LM = 13 and $n$ for SM = 20).

**Intrasexual contest behaviors**

A contest began when the males tried to face each other and extended their pedipalps downwards (Figs. 13, 14), which always was preceded by contact between the individuals ($n =$

**Fig. 14.** Male–male *Phalangium opilio* contest, movements after initial contact. Males extend their pedipalp downwards (black arrow shows the left pedipalp of the male on the left) and the chelicerae forwards (circle). White arrow shows the right leg I of the male on the right seconds before displaying legs I forward extension. Scale bar = 1 cm. **Fig. 15.** Male–male pedipalp contest. With their pedipalps extended downwards (black arrow shows the right pedipalp of the male on the left), they rapidly tap the opponent's pedipalp. Scale bar = 1 cm. **Fig. 16.** Male–male pedipalp contest and forward pushing, displaying legs I forward extension (white arrows). Scale bar = 1 cm. **Fig. 17.** Male–male contest showing an example of a possible ending. The male on the left subdued the male on the right by pushing. The latter fled seconds after being pushed. Scale bar = 5 mm.
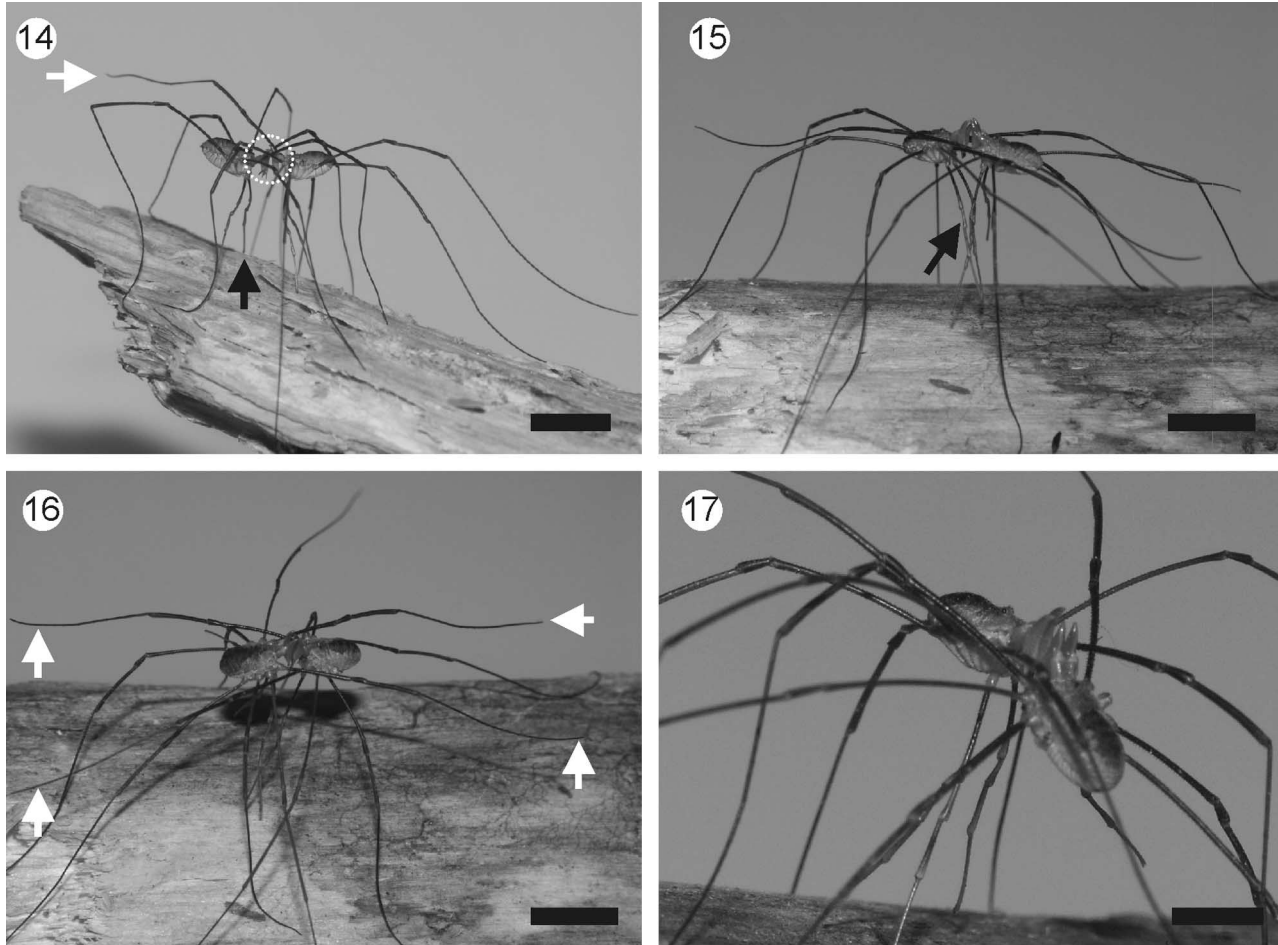


20 contests). The animals then extended the first segment of chelicerae, moving the second segment forward and positioning it perpendicular to the body and substrate, with the chelae opened. The cheliceral horns pointed forward–upwards (Figs. 14–16). Simultaneously, they extended both legs I forward, parallel to the substrate, resting them on trochanter and (or) femur of the contender's legs (legs I forward extension; $n = 14$ contests) (Figs. 13, 16).

With both pedipalps extended downwards, the animals moved them forward and backwards, one after the other, very fast and repeatedly, usually tapping the pedipalps of the contender (pedipalp contest; Figs. 13, 15, 16). In some contests, it was obvious that they pulled the contender's pedipalp towards themselves by abruptly flexing the trochanter–femur articulation ($n = 7$ contests), occasionally entwining one of his pedipalps with one of those of the contender ($n = 10$ contests). While displaying these pedipalpal movements, the two individuals gently touched the anterior chelicerae of one another and slowly pushed, by gradually extending legs IV and (or) III (forward pushing; $n = 13$; Figs. 13,

16). Among these 13 contests, in 11 cases the male that subdued the contender in pushing (Figs. 13, 17) won the contest. Once, a male that was winning lost (fled) immediately after having his pedipalp twisted, and another fled after being pinched with the chelicerae (see below). One male won after abruptly bouncing his body forward, hitting the contender's cheliceral horns with his. In another contest, forward pushing did not occur. Instead, these males of similar sizes gently touched their cheliceral horns against one another, rubbing the tips of their horns against the same region of the contender. This contest only ended after cheliceral pinching occurred. In total, cheliceral pinches were observed in just three contests, with the pinched individual fleeing (two cases: chelicera was pinched; one case: tarsus of pedipalp was pinched).

The median contest duration was 9.7 s (range = 4–87.6 s, $n = 20$). In the 13 contests in which it was possible to qualitatively determine which contender was larger, the larger individual, with larger cheliceral horns, won the contest. In the collective terraria, LM were seen pursuing SM with the

pedipalps extended downwards. We also observed LM pinching motionless SM on the dorsum with chelicerae. After a few days (<5) of cohabiting in the terraria, SM were systematically found dead, usually missing legs.

## Discussion

### Morphometrics

The dimorphic structures used in mate choice or competition for mates among sexually dimorphic species often have allometric growth, in which a small increase in body size results in a great increase of sexually dimorphic structures (see Eberhard and Gutierrez 1991; Eberhard et al. 1998). The allometric growth patterns of *P. opilio* may have evolved from selective pressures related to intra- and inter-sexual interactions.

Plots of body size for sexually dimorphic males usually show a normal, Gaussian pattern (e.g., Moczek and Emlen 2000), as was shown with the *P. opilio* sampled here. The pattern for male dimorphic structures varies a lot according to the species, being normal, skewed towards larger or smaller structures, or bimodal (Zeh 1987; Eberhard and Gutierrez 1991). This has important ecological implications, since for species that follow a bimodal pattern, males may adopt distinct strategies according to their body and weapon size (Moczek and Emlen 2000). Males with smaller pedipalps and chelicerae were more abundant in our samples. Though smaller males appear earlier in the season in some species (Eberhard 1980), adult *P. opilio* are found throughout summer, autumn, and the beginning of winter (Jones et al. 1990). Since the animals used in this study were collected at the end of summer and in the first 2 months of autumn, it is not obvious to attribute our results to a difference in the ontogeny of males. Another possible explanation is the sample size, though a similar pattern to what we found was reported for some male beetles that bear a sternal spine used in male–male contests with 129 measured animals (Eberhard and Gutierrez 1991). Finally, it is possible that suboptimal field conditions produced males with smaller dimorphic structures that specific year (see Cook 1990).

### Sexual dimorphism and intrasexual interactions

The frontal region of male *P. opilio* chelicerae constitutes the area where they push each other in contests, just like deer use their antlers and some beetles use their horns (Andersson 1994), leading us to argue that the cheliceral horns of *P. opilio* may be a structure to increase leverage by which males can better apply their strength to push a contender. An alternative but nonexclusive explanation is that males assess cheliceral horn size while forward pushing. The cheliceral horns of the two contenders are always in contact during this behavior. The sensilla chaetica (contact mechanoreceptor, Willemart and Gnaspini 2003) present on the integument could provide information on who has longer cheliceral horns. Moreover, in one occasion males repeatedly touched their cheliceral horns without displaying forward pushing. Because there is a correlation between body size and horn size, assessing cheliceral horn size could be an indication of the size of the contender and thus of strength (and possibly fitness). This is known to occur among several taxa. Toads, an acoustic animal, seem to identify the contender's size by the sound of the croaks (Da-

vies and Halliday 1978). Stalked-eyes flies, a visual animal, compare the size of their head projections, which are an honest signal of their body size (Panhuis and Wilkinson 1999). Similarly, harvestmen, animals highly dependent on contact (Macías-Ordóñez 1997), could be, in addition to pushing each other, comparing the size of their cheliceral horns by touching the contender's horns.

The pedipalp contest involves highly repeated tapping, attempts to pull the contender's pedipalp towards their own body, and twisting. Perhaps one purpose is to twist the opponent's pedipalp. Harvestmen are nonvisual animals (Macías-Ordóñez 1997), and pedipalps are not equipped with trichobothria ("wind receptors"; Barth 2002), and thus tapping is the only way they have to know the contender's pedipalp location and thus be able to twist it. Sensilla chaetica on the pedipalp would be responsible for this contact detection. Leaving the pedipalp stationary possibly makes it easier to be caught and twisted by the opponent, and pulling the contender's pedipalp would be frustrated attempts to twist it. In this context, longer pedipalps would be more efficient to grab and twist the contender's pedipalp and possibly allow tighter twisting.

Therefore, hypothesis 1 (cheliceral horns and the longer pedipalps are of use in male–male contests) was corroborated by our data. Several cues would be important during male–male contests. For example, overall strength would be assessed by forward pushing (indeed, in 11 out of 13 cases in which it occurred, winners of the pushing won the contest). Stronger males are expected to be superior in this behavior, which seems to be helped by the locking provided by legs I forward extension. Comparing the size of the horns could be a redundant assessment of overall strength or a way to assess the size of the contender before starting pushing, as observed in one case. During pedipalp contest, it appears that rapidity, length, and strength of the pedipalp might play a role, since these three features possibly help to twist the contender's pedipalp accurately. In some cases, males fought by other rules, pinching the contender with chelicerae. In the three cases this behavior was observed, it proved to be a good strategy, since the pinched individuals fled as soon as they were able to release themselves from the pinching.

Finally, by showing that pedipalps and cheliceral horns have a function, the possibility that these structures are simply a product of allometric growth, are functionless and selectively neutral, and are a result of selection for larger males, can now be discarded (see Gould 1977; Gould and Lewontin 1979).

### Why interact aggressively with other males?

Simon (1879) wrote that "A l'époque de la reproduction, les mâles se livrent des combats acharnés, qui ont été observés chez *Phalangium Opilio* [sic]" (*P. opilio* males engage in fierce male–male contests in the reproductive period), but did not mention any further detail. Male–male contests in this study were observed without females nearby, the latter neither used the arenas (thus no latent chemical cues were present) nor had physical contact with the test males for at least 5 days prior to the observations. We can therefore infer that there is no need of female stimuli for males to interact aggressively. Perhaps they engage in con-

tests for territories, though we have no evidence to support this idea. Females lay eggs on several distinct substrates, such as under rocks, in cracks in the soil, and even on plants. They feed on a variety of items, plant and animal matter, live or dead (Bristowe 1949; Butcher et al. 1988; Morse 2001). Therefore, there is no obvious site that males could use as territory, as known in some arthropod species (oviposition sites: Macías-Ordóñez 1997; feeding sites: Eberhard 1998). Because we often found several *P. opilio* on some trees and low vegetation during the reproductive period but none in other similar locations (same plant species), females could be choosing winners of contests indirectly within these groups (Wiley and Poston 1996).

Further studies in the field should be conducted for us to understand not only why male–male contests occur but also if LM and SM have distinct reproductive strategies (since SM tend to loose contests but are abundant in the population; see Eberhard 1982; Moczek and Emlen 2000). In beetles, smaller individuals may emerge earlier in the season or disperse more, possibly avoiding larger rivals (Eberhard 1980). Fleeing seems to be an adaptive behavior after loosing a contest to LM, since these systematically killed SM in close terraria. In contrast, female were not found dead in communal terraria. Female remating frequency seems high, since in unrecorded video observations the same couple copulated five times in two hours. However, as sperm precedence in this species has never been studied, we do not know if males could be displacing other males in specific locations to increase their probability of being the first to copulate with females.

### Sexual dimorphism and intersexual interactions

Assessment of morphological features in harvestmen has to be through contact (see Otte and Stayman 1979). As these animals actively move their legs I and II to explore the environment (Willemart and Gnaspini 2003), one could expect females to use them to touch the male's cheliceral horns and long pedipalps to assess male size. Though this did not occur, we cannot discard the possibility that females might evaluate pedipalp size by detecting whether the male is holding her by legs III or IV, since this proved to be related to the male's size. Cheliceral horns could be evaluated when they eventually contacted the female's dorsum after copulation resumed. Therefore, these sexually dimorphic structures may be used by females to assess the male's quality.

Another possibility allied with the one above is that male structures are used to achieve successful copulation by helping to hold the female (see references in Thornhill and Alcock 1983; Eberhard 1996; Hume et al. 2005). Larger *P. opilio* males, having longer pedipalps, held females by legs IV, whereas SM did so by legs III. Since the female is pulled against the male's body during sexual interactions, having the grip at more posterior regions is probably more efficient at reducing the female's mobility, though no difference between LM and SM concerning female movements could be detected in our study. Interestingly, males of other Eupnoi species, which do not have sexually dimorphic longer pedipalps, hold females by legs II (e.g., Bishop 1949; Edgar 1971; Macías-Ordóñez 1997). Thus, comparative data also suggest that longer pedipalps gives males of *P. opilio* a steadier grip.

Long cheliceral horns could theoretically be used to minimize the possibility that females will roll over the body of males, but this could not be verified in our observations. However, in cases when females remained quiet, males always displayed prosoma inclination following copulation, positioning themselves in a way that their cheliceral horns remained approximately parallel to the longitudinal axis of the female. This behavior has not been recorded in other species, and we cannot state its function. Perhaps brief contact of the cheliceral horns on the female's dorsum would communicate that the male is above her and thus stimulate her to remain quiet.

Our hypothesis 2 is therefore also corroborated (i.e., the horns of chelicerae and the longer pedipalps are of use in intersexual interactions). The fact that these structures are also used in male–male contests poses no problems for our explanations, since structures may evolve in one context and subsequently be used in other ones (Eberhard 1979).

### Coercion, persuasion, and courtship

Inferences on mating success and the best male strategies to successfully copulate are difficult to make with our data. First of all, we cannot be sure whether the male successfully copulated when penetration occurred (see above). Moreover, we collected the animals as adults and consequently cannot know the reproductive status (number of previous matings, for example) of the females, which may influence female behavior.

On several occasions, both before and during copulation, *P. opilio* females displayed bouncing movements or more rarely tried to break the grip of the male by rolling over him. In these cases, it appears that holding females firmly was a requisite to allow successful copulation, since otherwise females would have fled. Bouncing movements can be interpreted either as an attempt to flee and thus minimize the costs of mating (sexual conflict; Arnqvist and Rowe 1995) or as a way to test the ability of the male to maintain contact with her and thus select for stronger males (indirect mate choice by screening; Eberhard 2002). These nonexclusive hypotheses are hard to distinguish (Shine et al. 2005), and further studies would be needed to test them.

In some cases females resisted and in others they did not, but males always displayed forelegs stroke both before and during copulation (Figs. 10, 11), characterizing a precopulatory and copulatory courtship. Therefore, with (when females displayed bouncing movements) or without (when females remained quiet) coercion–persuasion by the male, tactile courtship always occurred. This behavior might have the function of increasing the probability that females will allow the male to start copulation. Examples among harvestmen would be *Platybunus bucephalus* (Koch, 1835) and *Leiobunum nigripes* Weed, 1887. Males have been reported to tap the genital operculum of females, after which the latter opens it and allow males to penetrate (Immel 1955; Shultz 2005). Other possible functions of courtship may be to delay copulation and thus allow more sperm to be transferred or to influence cryptic female choice (Eberhard 1996, 2002).

The same discussion is valid for the observed penis rubbing on female's mouth. Macías-Ordóñez (1997) also reported it in *Leiobunum vittatum* (Say, 1821), though not before but during copulation, between intromissions. It is

not clear that besides the mechanical stimulation, males also are offering secretions from their penis to the females. However, Kästner (1935) reported that *Opilio parietinus* (De Geer, 1778) females groom with a liquid in their mouth after copulation. Shultz (2005) recently reported *Leiobunum* males offering secretions to females before copulation. *Phalangium opilio* females groom their chelicerae after copulation exactly as they do after feeding, leading us to believe that some secretion is offered.

## Acknowledgements

## References

Allard, C.M., and Yeargan, K.V. 2005. Diel activity patterns and microspatial distribution of the harvestman *Phalangium opilio* (Opiliones, Phalangiidae) in soybeans. J. Arachnol. **33**: 745–752. doi:10.1636/T04-17.1.

Andersson, M. 1994. Sexual selection. Princeton University Press, Princeton, N.J.

Arnqvist, G. 1989. Sexual selection in a water strider: the function, nature of selection and heritability of a male grasping apparatus. Oikos, **56**: 344–350.

Arnqvist, G., and Rowe, L. 1995. Sexual conflict and arms races between the sexes: a morphological adaptation for control of mating in a female insect. Proc. R. Soc. Lond. B Biol. Sci. **261**: 123–127.

Barth, F.G. 2002. A spider's world: senses and behavior. Springer-Verlag, Berlin.

Bateman, P.W. 2000. The influence of weapon asymmetry on male–male competition success in a sexually dimorphic insect, the African king cricket *Libanasidus vittatus* (Orthoptera: Anostostomatidae). J. Insect Behav. **13**: 157–163. doi:10.1023/A:1007775928411.

Bishop, S.C. 1949. The function of the spur on the femur of the palpus of the male *Leiobunum calcar* (Wood) (Arachnida: Phalangida). Entomol. News, **60**: 10–11.

Bristowe, W.S. 1949. The distribution of harvestmen (Phalangida) in Great Britain and Ireland, with notes on their enemies and food. J. Anim. Ecol. **18**: 100–114.

Butcher, M.R., Penman, D.R., and Scott, R.R. 1988. Field predation of two spotted spider mite in a New Zealand strawberry crop. Entomophaga, **33**: 173–183. doi:10.1007/BF02372652.

Candolin, U. 2003. The use of multiple cues in mate choice. Biol. Rev. **78**: 575–595. doi:10.1017/S1464793103006158. PMID:14700392.

Claus, C., and Moquin-Tandon, G. 1884. Traité de Zoologie. Libraire F Savy, Paris.

Clingenpeel, L.W., and Edgar, A.L. 1966. Certain ecological aspects of *Phalangium opilio* (Arthropoda: Opiliones). Pap. Mich. Acad. Sci. Arts Lett. **51**: 119–126.

Cook, D.F. 1990. Differences in courtship, mating and postcopulatory behaviour between male morphs of the dung beetle *Onthophagus binodis* Thunberg (Coleoptera: Scarabeidae). Anim. Behav. **40**: 428–436. doi:10.1016/S0003-3472(05)80522-6.

Darwin, C. 1871. The descent of man and selection in relation to sex. Murray, London.

Davies, N.B., and Halliday, T.R. 1978. Deep croaks and fighting assessments in toads *Bufo bufo*. Nature (London), **275**: 683–685.

de Graaf, H.W. 1882. Sur la construction des organes génitaux des Phalangiens. E.J. Brill, Leiden, the Netherlands.

Eberhard, W.G. 1979. The function of horns in *Podischnus agenor* (Dynastinae) and other beetles. *In* Sexual selection and reproductive competition in insects. *Edited by* M.S. Blum and N.A. Blum. Academic Press, New York. pp. 231–258.

Eberhard, W.G. 1980. Horned beetles. Sci. Am. **242**: 166–182.

Eberhard, W.G. 1982. Beetle horn dimorphism: making the best of a bad lot. Am. Nat. **119**: 420–426. doi:10.1086/283920.

Eberhard, W.G. 1996. Female control: sexual selection by cryptic female choice. Princeton University Press, Princeton, N.J.

Eberhard, W.G. 1998. Sexual behavior of *Acanthocephala declivis guatemalana* (Hemiptera: Coreidae) and the allometric scalling of their modified hind legs. Ann. Entomol. Soc. Am. **91**: 863–871.

Eberhard, W.G. 2002. Female resistance or screening? Male force versus selective female cooperation in intromission in sepsid flies and other insects. Rev. Biol. Trop. **50**: 485–505. PMID:12298280.

Eberhard, W.G., and Gutierrez, E. 1991. Male dimorphism in beetles and earwigs and question of developmental constraints. Evolution, **45**: 18–28. doi:10.2307/2409478.

Eberhard, W.G., Huber, B.A., Rodriguez, R.L., Briceno, D., Salas, I., and Rodriguez, V. 1998. One size fits all? Relationships between the size and degree of variation in genitalia and other body parts in twenty species of insects and spiders. Evolution, **52**: 415–431. doi:10.2307/2411078.

Edgar, A.L. 1971. Studies on the biology and ecology of Michigan Phalangida (Opiliones). Univ. Mich. Mus. Zool. Misc. Publ. **144**: 1–64.

Edgar, A.L. 1990. Opiliones (Phalangida). *In* Soil biology guide. *Edited by* D.L. Dindal. John Wiley and Sons, New York. pp. 529–581.

Edgar, A.L., and Yuan, H.A. 1968. Daily locomotory activity in *Phalangium opilio* and seven species of *Leiobunum* (Arthropoda: Phalangida). Bios, **39**: 168–176.

Emlen, D.J. 2001. Costs and the diversification of exaggerated animal structures. Science (Washington, D.C.), **291**: 1534–1536. doi:10.1126/science.1056607. PMID:11222856.

Gould, S.J. 1977. Ever since Darwin: reflections in natural history. W.W. Norton, New York and London.

Gould, S.J., and Lewontin, R.C. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. Proc. R. Soc. Lond. B Biol. Sci. **205**: 581–598.

Hebets, E.A. 2004. Attention-altering signal interactions in the multimodal courtship display of the wolf spider *Schizocosa uetzi*. Behav. Ecol. **16**: 75–82. doi:10.1093/beheco/arh133.

Hebets, E.A., and Papaj, D.R. 2005. Complex signal evolution: developing a framework of testable hypotheses. Behav. Ecol. Sociobiol. **57**: 197–214. doi:10.1007/s00265-004-0865-7.

Hume, K.D., Elwood, R.W., Dick, J.T.A., and Morrison, J. 2005. Sexual dimorphism in amphipods: the role of male posterior

gnathopods revealed in *Gammarus pulex*. Behav. Ecol. Sociobiol. **58**: 264–269. doi:10.1007/s00265-005-0925-7.

Immel, V. 1955. Einige Bemerkungen zur Biologie von *Platybunus bucephalus* (Opiliones, Eupnoi). Zool. Jahrb. Abt. Syst. **83**: 475–484.

Jones, D., Ledoux, J.C., and Emerit, M. 1990. Guide des araignées et des opilions d'Europe. Delachaux et Niestlé, Lausanne, Switzerland.

Juen, A., and Traugott, M. 2004. Spatial distribution of epigaeic predators in a small field in relation to season and surrounding crops. Agric. Ecosyst. Environ. **103**: 613–620.

Kästner, A. 1928. Opiliones (Weberknechte, Kanker). *In* Die Tierwelt Deutschlands und der angrenzenden Meeresteile nach ihren Merkmalen und nach ihrer Lebensweise. *Edited by* F. Dahl. Verlag von Gustav Fischer, Jena, Germany. pp. 1–51.

Kästner, A. 1931. Biologische Beobachtungen an Phalangiiden. Zool. Anz. **95**: 293–302.

Kästner, A. 1935. Opiliones Sundervall, Weberknechte. *In* Handbuch der Zoologie, Bd. III, Zweite Hälfte. *Edited by* W. Kukenthal and T. Krumbach. Walter de Gruyter and Co., Berlin. pp. 300–393.

Lennis, J. 1886. Snnophs der drei naturreiche: ein handbuch für höhere Lehranstalten Hannover. Bahnische Buchhandlung.

Macías-Ordóñez, R. 1997. The mating system of *Leiobunum vittatum* Say 1821 (Arachnida: Opiliones: Palpatores): resource defense polygyny in the striped harvestman. Ph.D. thesis, Lehigh University, Bethlehem.

Moczek, A.P., and Emlen, D.J. 2000. Male horn dimorphism in the scarab beetle, *Ontophagus taurus*: do alternative reproductive tactics favour alternative phenotypes? Anim. Behav. **59**: 459–466. doi:10.1006/anbe.1999.1342. PMID:10675268.

Moore, A.J. 1990. The evolution of sexual dimorphism by sexual selection: the separate effects of intrasexual selection and intersexual selection. Evolution, **44**: 315–331. doi:10.2307/2409410.

Mora, G. 1990. Paternal care in a neotropical harvestman, *Zygopachylus albomarginis* (Arachnida, Opiliones: Gonyleptidae). Anim. Behav. **39**: 582–593. doi:10.1016/S0003-3472(05)80425-7.

Morse, D. 2001. Harvestmen as commensals of crab spiders. J. Arachnol. **29**: 273–275.

Otte, D., and Stayman, K. 1979. Beetle horns: some patterns in functional morphology. *In* Sexual selection and reproductive competition in insects. *Edited by* M.S. Blum and N.A. Blum. Academic Press, New York. pp. 259–292.

Panhuis, T.M., and Wilkinson, G.S. 1999. Exaggerated male eye span influences contest outcome in stalk-eyed flies (Diopsidae). Behav. Ecol. Sociobiol. **46**: 221–227. doi:10.1007/s002650050613.

Planet, L. 1905. Histoire naturelle de la France. 14e partie. Les fils d'Émile Deyrolle, Paris.

Perrier, R. 1929. Cours élémentaire de Zoologie. Masson et cie, Paris.

Savory, T.H. 1962. Daddy longlegs. Sci. Am. **207**: 119–128.

Shine, R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. Q. Rev. Biol. **64**: 419–461. doi:10.1086/416458. PMID:2697022.

Shine, R., Wall, M., Langkilde, T., and Mason, R.T. 2005. Do female garter snakes evade males to avoid harassment or to enhance mate quality? Am. Nat. **165**: 660–668. doi:10.1086/429591. PMID:15937746.

Shultz, J.W. 2005. Preliminary analysis of mating in *Leiobunum nigripes* (Opiliones) and diversification of male reproductive structures in *Leiobunum*. News. Am. Arachnol. Soc. **72**: 11.

Simon, E. 1879. Arachnides de France. Librarie Encyclopedique de Roret, Paris.

Sneddon, L.U., Huntingford, F.A., and Taylor, A.C. 1997. Weapon size versus body size as a predictor of winning in fights between shore crabs, *Carcinus maenas* (L.). Behav. Ecol. Sociobiol. **41**: 237–242. doi:10.1007/s002650050384.

Stanek, V.J. 1964. Le monde animal en 1001 photos. Hachette, Tchecoslovaquie.

Thornhill, R., and Alcock, J. 1983. The evolution of insect mating systems. Harvard University Press, Cambridge, Mass.

Wiley, R.H., and Poston, J. 1996. Indirect mate choice, competition for mates, and coevolution of the sexes. Evolution, **50**: 1371–1381. doi:10.2307/2410875.

Willemart, R.H., and Gnaspini, P. 2003. Comparative density of hair sensilla on the legs of cavernicolous and epigean harvestmen (Arachnida, Opiliones). Zool. Anz. **242**: 353–365.

Williams, G. 1962. Seasonal and diurnal activity of harvestmen (Phalangida) and spiders (Araneida) in contrasted habitats. J. Anim. Ecol. **31**: 23–42.

Zar, J.H. 1999. Biostatistical analysis. 4th ed. Prentice-Hall Inc., Upper Saddle River, N.J.

Zeh, D.W. 1987. Life history consequences of sexual dimorphism in a chernetid pseudoscorpion. Ecology, **68**: 1495–1501. doi:10.2307/1939233.