

# Coercive copulation in two sexually cannibalistic camel-spider species (Arachnida: Solifugae)

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## Keywords

courtship; luring behaviour; sexual coercion; reproduction.

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## Introduction

In promiscuous mating systems, males and females have different optimal mating rates. These different rates, typically lower for females than for males (Trivers, 1972; Andersson, 1994), lead to conflict over the control of reproduction. Males may use a number of tactics to overcome female resistance to mating, including (1) luring/courtship; (2) coercion/forced copulation (Clutton-Brock & Parker, 1995; Alexander, Marshall & Cooley, 1997; Eberhard, 2002).

During luring or courtship, females are generally active participants and can choose among competing males as mating partners (Andersson, 1994; Brown, Crespi & Choe, 1997). Males typically perform luring behaviour before copulation to reduce female resistance and to facilitate copulation; this is known as pre-copulatory courtship. However, males can also sexually stimulate the female during or after copulation (Eberhard, 1996). Such copulatory courtship is favoured by sexual selection to facilitate sperm competition and enhance male fertilization success (Ben-Ari, 2000; Simmons, 2005). Courtship behaviours are also suggested as a means of reducing aggressive tendencies in a potentially dangerous mate and to reduce the cost of mating to the male (Alexander *et al.*, 1997).

Coercion can be used by males to achieve mating with females that would not otherwise be receptive to copulation

## Abstract

Males can overcome female resistance to mating either by using luring behaviour or through sexual coercion. We studied mating behaviour in two sexually cannibalistic camel-spider species *Galeodes caspius subfuscus* (Galeodidae) and *Gluvia dorsalis* (Desiidae), to determine the presence of luring and/or coercive traits. Several behavioural features demonstrate coercive mating in the two species: (1) males used strength or fast movement to grab a female; (2) males prevented female counter-attack and escape; (3) males injured the female during coercive copulations; (4) females struggled to interrupt mating. The mode of mating differed considerably. In *Galeodes*, but not in *Gluvia*, males induced an immobile state in females. Despite the presence of coercive mating that caused injuries to females, *Galeodes* males also engaged in courtship behaviours before copulation (stroking with pedipalps) and during copulation (stroking and tapping). The occurrence of pre-copulatory courtship in coercively mating males has not been reported before. In *Gluvia*, coercive traits suggest that forced copulation is the exclusive mating strategy. Coercive mating strategies in camel-spiders may have evolved as an anti-predation strategy, as sexual cannibalism occurred in *c.* 40% of all sexual interactions.

(Clutton-Brock & Parker, 1995). Forced copulation is widespread in a variety of animal species both among vertebrates and among invertebrates (Thornhill & Alcock, 1983; Vahed, 2002; Peretti & Willemart, 2007; Johns *et al.*, 2009), whereby males apply physical, behavioural or physiological adaptations to overcome female resistance (Brown *et al.*, 1997). In some species, an additional benefit from forced copulation can be reduced energy expenditure due to the absence of courtship. Male courtship costs may include direct energetic costs, loss of foraging opportunities, increased predation risk (Stuart-Fox & Whiting, 2005) or physical injury from encounters with cannibalistic females (Arnqvist & Henriksson, 1997). Thus, males would not perform luring behaviour before, during or after copulation once coercion/forced copulation has evolved (Brown *et al.*, 1997). However, the strategies are not mutually exclusive and coercion could coincide with copulatory courtship (Vahed, 2002; Peretti & Willemart, 2007).

Sexual cannibalism, in which the female may attack or consume the male during a sexual encounter, introduces an additional level of conflict between the sexes (Elgar, 1992). The risk of sexual cannibalism is expected to favour counter-adaptation in males in the form of courtship, opportunistic matings, coercive copulation or anti-predatory traits such as feigning death or the induction of paralysis in females (Elgar, 1992; Alexander *et al.*, 1997; Fromhage & Schneider, 2005; Bilde *et al.*, 2006). Here, we investigate coercion as a

counter adaptation to sexual cannibalism in camel-spiders (Solifugae) that belong to the arachnids, a group in which cannibalism is common (Elgar, 1992; Hrušková-Martišová, Pekar & Gromov, 2007).

Mating behaviour in camel-spiders has been described in only a few species (Amitai, Levy & Shulov, 1962; Junqua, 1966; Muma, 1966; Cloudsley-Thompson, 1967; Punzo, 1997). In these species, mating behaviour does not include courtship. The female is grasped forcibly by the male, which releases a spermatophore and inserts it into the genital opening of the female. Subsequently, the pair separates and the male moves away quickly (Muma, 1966). Although some behavioural components of this process are broadly similar among distantly related camel-spider taxa (mating position or spermatophore transfer), exceptions occur. One example is the induction of a state of immobility in females (Junqua, 1966; Wharton, 1987) or male stroking of the female with its pedipalps during mating (Amitai *et al.*, 1962; Cloudsley-Thompson, 1967; Wharton, 1987).

We studied the mating behaviour of two distinct camel-spider species: *Galeodes caspius subfuscus* (Birula) (Solifugae: Galeodidae) and *Gluvia dorsalis* (Latreille) (Solifugae: Desiidae). The mating behaviour of *G. caspius subfuscus* was first described by Heymons (1902). Mating behaviour in representatives of the family Desiidae has not been studied. By detailed analysis of the qualitative and quantitative aspects of the mating behaviour, we aimed to describe and compare the mating strategies used by the two species. In particular, we were interested in luring, coercive behavioural traits and the potential costs to each sex from forced copulation. Using comparative intersexual morphological analysis, we examine how coercive behavioural traits are linked to morphology in both sexes with respect to the mating tactics used by these species.

## Materials and methods

*Galeodes caspius subfuscus* is one of the most common and largest (body length up to 7 cm) camel-spider species in central Asia, whereas *G. dorsalis* is a small (body length 2 cm) western European species occurring on the Iberian Peninsula. Both species are nocturnal and forage on the ground (Hrušková-Martišová *et al.*, 2007; M. Hrušková-Martišová, unpubl. data).

Fifteen males and 13 females of *Galeodes* were collected from the slopes and plains of the Taukum semi-desert (Kapschagay, south-east Kazakhstan) in June 2005. Adult *Gluvia* (39 males, 21 females) were collected from grassy plains near Évora (southern Portugal) in June 2006. Camel-spiders were identified according to Birula (1938) and Rambla & Barrientos (1986). Males were identified by the presence of flagellum; females were identified by the development of the genital opening. Camel-spiders were kept separately in plastic vials (12 cm long, 2 cm diameter for *Galeodes*; 6 cm long, 1.5 cm diameter for *Gluvia*), provided with a piece of wet paper to maintain humidity, and kept in captivity for 2 days.

All females were fed *ad libitum* with locusts and crickets a few hours before using them in experiments to minimize cannibalistic tendencies. Mating experiments were performed early in the night.

To observe mating, we placed a female in a mating arena (plastic box 20 × 15 × 6 cm for *Galeodes*, 17 × 3 × 4 or 6 × 1.5 × 1.5 cm for *Gluvia*) 30 min before a male was introduced. We used the dim white light of a torch to illuminate the mating arena. Intersexual interactions that followed were recorded on a video camera (Canon MV350). The pairs were observed until an interaction (either reproductive or cannibalistic) had ended or were separated if none of these appeared within 5 min. Intersexual interaction was considered as a mating attempt if the male performed courtship or grasped hold of the female for > 5 s.

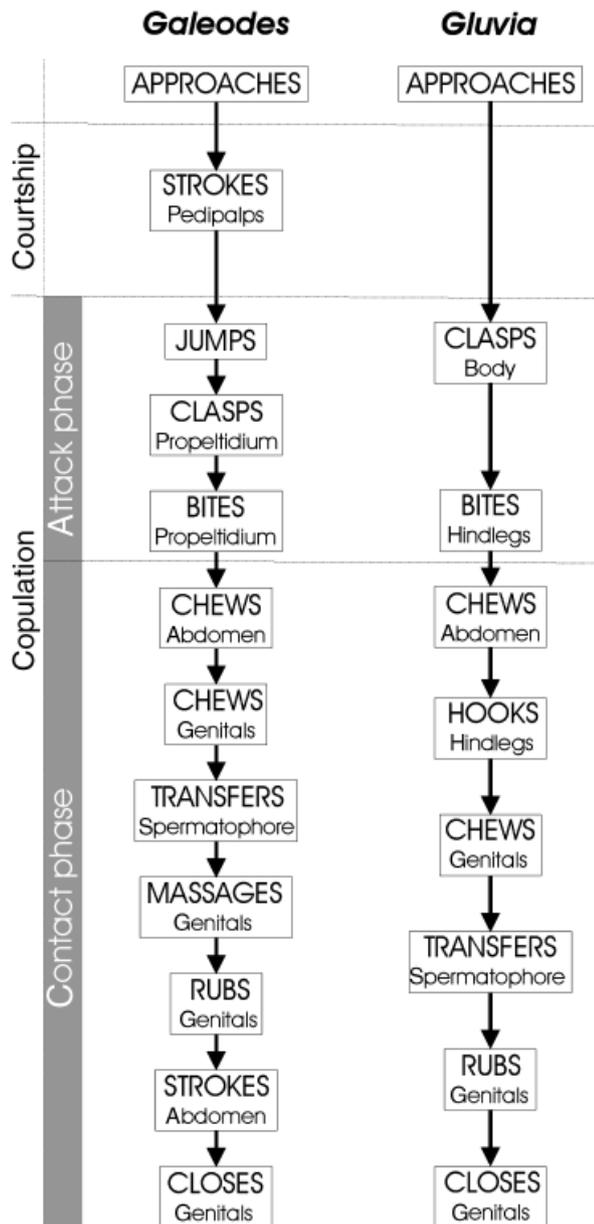
The reproductive status of the collected individuals was not known. But because we collected at the beginning of the mating season and found no signs of coercive mating (scars on the propeltidium, legs and abdomen of females), we assumed that the females were virgin. In *Galeodes*, all intersexual interactions resulted in mating attempts (13 different pairs). Three of five of these mated females copulated with an additional male within 2 days. In *Gluvia*, 20 intersexual interactions out of 69 resulted in mating. All inseminated females were presented with an additional male, but only in two cases was re-mating completed. In both species, males were used repeatedly.

The recorded behavioural interactions were analysed frame-by-frame using PINNACLE STUDIO version 9.3.6 software (Pinnacle Systems Inc., Mountain View, CA, USA). In both species, the main behavioural events of courtship and mating were identified and described according to Muma (1966): (1) the attack phase (assault of a female by the male); (2) the contact phase (adoption of the mating position); (3) the release phase (the male flees from the female). Before and/or within these phases, we recognized luring and coercive traits. Luring traits were distinguished as pre-copulatory (before) and copulatory courtship (after or during sperm transfer). Coercive traits included behaviours such as clasping, struggling and biting.

Measurements of morphological traits (from 10 individuals each of both species and both sexes) were conducted using a stereo microscope. Measurements included the shape and size of the chelicerae, the length and spination of pedipalps and the length of the hind legs. A Wilcoxon rank-sum test was used to compare the morphological characteristics between sexes. We tested the prediction that adaptive morphological traits in males for coercive matings have evolved differences in size or shape from those of females. Mean values below are given ± 1 SE.

## Results

Mating behaviour differed markedly between the two species and was more complex in *Galeodes* than in *Gluvia* (Fig. 1, see also supporting information video S1 and S2). Within species, the sequence of the main behavioural events showed little variation. In both species, mating began after



**Figure 1** Flow diagram of the main behavioural events performed by males of *Galeodes caspius subfuscus* and *Gluvia dorsalis* during mating. The events displayed occurred between mutual encounter and the retreat phase.

an encounter and ended suddenly with the male fleeing the female (the release phase).

### Pre-copulatory cannibalism

In *Galeodes*, in five of 13 intersexual interactions (38.5%), the female counter-attacked and subsequently consumed the male before mating. Similarly, 26 of 69 interactions in *Gluvia* (37.7%) resulted in sexual cannibalism.

### Pre-copulatory courtship

Male *Galeodes* slowly approached the female frontally with raised pedipalps and touched her with the pedipalps. He then started to stroke the distal part of the female's pedipalps gently, with his pedipalps continuously outspread. Initially, the female responded to a male's approach with an agonistic posture (raised pedipalps, open chelicerae and stridulation), but subsequently, she reciprocated his stroking. No courting behaviour was observed in *Gluvia*.

### Attack phase

In all observed cases, *Galeodes* males used pedipalps to force the female's pedipalps to the ground in a sudden move. A male then stuck one of his suctorial organs (at the tips of the pedipalps) onto her propeltidium (i.e. forepart of carapax) and jumped over her chelicerae. Male pedipalps were 64% longer than those of females (Wilcoxon's test,  $P < 0.0001$ , Table 1). The longer pedipalps helped males maintain a safe distance from female chelicerae during the jump. After jumping, the male clasped the female's prosoma with his pedipalps laterally, thereby preventing the female from pointing her chelicerae towards him in a counter-attack (Fig. 2a). Immediately after clasping the female, the male bit the lateral part of her propeltidium (between the coxae of the legs) with his chelicerae. This resulted in the male cheliceral fingers piercing and injuring the cuticle of all mounted females (Fig. 3a). Morphological analysis showed that the males' cheliceral fingers were more bent than those of females (Fig. 4a, b). Subsequent to the bite, the female immediately ceased all movement and fell into an immobile state, in which her pedipalps and the first pair of legs moved slowly up in a spasm. This immobile state persisted throughout copulation.

In *Gluvia*, the male would run after the female and lunge quickly towards her from the rear left (44%), the rear right (34%) or behind (22%,  $n = 18$ ). The rearmost legs of males were 67% longer than those of females (Wilcoxon's test,  $P = 0.0004$ , Table 1). The length of the pedipalps was similar in both sexes (Wilcoxon's test,  $P = 0.12$ , Table 1). Males clasped the female's body and bit her hind leg. This bite seriously injured the female's leg, causing necrosis (Fig. 3b) in four of 20 encounters (20%). In *Gluvia*, the female never fell into an immobile state.

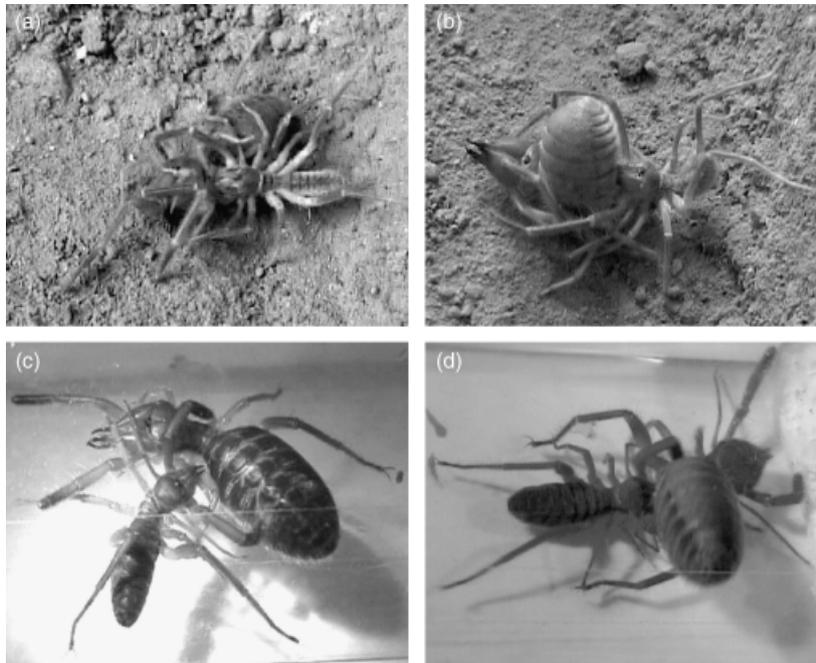
### Contact phase

While tapping the immobile female with his pedipalps, a *Galeodes* male began to chew her abdominal cuticle lightly. The chewing lasted for  $43.6 \pm 21$  s ( $n = 6$ ). He then folded her abdomen over her propeltidium, resulting in the copulatory position. In this posture, he inserted the fixed (i.e. lower) cheliceral fingers into the female's genital opening and chewed the genitals (pre-spermatophore transfer massage) for  $36.2 \pm 18.6$  s ( $n = 6$ ). At the same time, the male clasped the entire female body with his pedipalps and forelegs (Fig. 2b). In males, the ventral femora and tibiae of the pedipalps have many long spines (Fig. 5), which remain

**Table 1** Comparison of selected morphological traits in males and females of the two study species

Morphological character	Galeodes		Gluvia	
	Males	Females	Males	Females
Width of propeltidium (mm)	8.5 (0.16)	10.9 (0.82)	2.77 (0.11)	4.87 (0.13)
Length of fixed cheliceral finger (mm)	6.5 (0.07)	8.5 (0.11)	1.27 (0.03)	2.22 (0.07)
Length of the untoothed finger (mm)	2.2 (0.04)	1.9 (0.07)	1.03 (0.02)	0.94 (0.04)
Length of pedipalp (mm)	54.8 (1.38)	42.8 (1.16)	15.1 (0.22)	15.9 (0.35)
Number of ventral spines on pedipalpal Fe	9	3	0	0
Number of ventral spines on pedipalpal Ti	8	8	0	0
Length of spines on pedipalpal Fe (mm)	4.2 (0.11)	2.7 (0.22)	–	–
Length of spines on pedipalpal Ti (mm)	3.2 (0.12)	1.8 (0.14)	–	–
Length of hind legs (mm)	–	–	24.7 (0.34)	23.1 (0.6)

Means and standard errors of the mean (in parentheses) are given for almost all characters.  $n=10$  for each character presented.



**Figure 2** Attack phases (a, c) and copulatory positions (b, d). (a) A *Galeodes caspius subfuscus* male clasps the female with pedipalps and bites the lateral side of her propeltidium. (b) A *G. caspius subfuscus* male clasps the female's folded body and chews her genitals. (c) A *Gluvia dorsalis* male clasps the female with pedipalps and bites her hind leg. (d) A *G. dorsalis* male hooks the female's hind legs and chews her genitals.

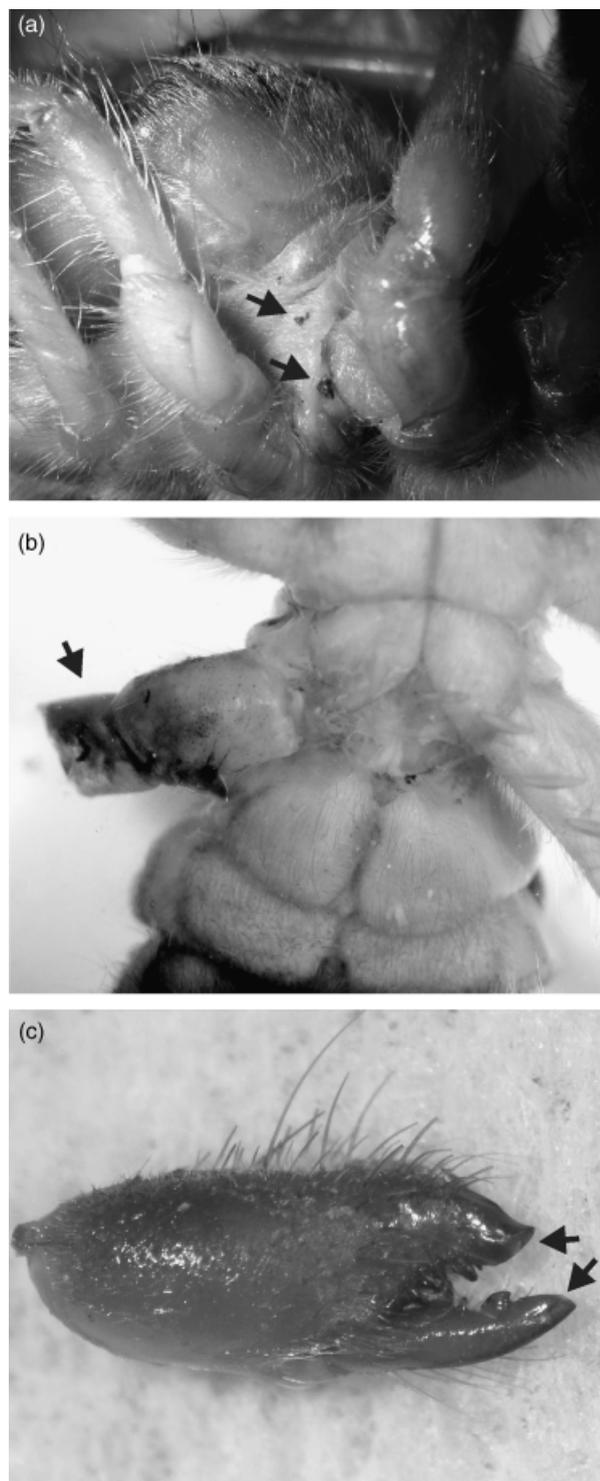
pressed against both sides of the female abdomen during copulation. Females have fewer spines on femora, and these were less prominent and significantly shorter than those in males (Wilcoxon's test,  $P < 0.0001$ , Table 1).

*Gluvia* males clasped the female and began to chew her abdominal cuticle without piercing it. After several seconds of chewing, the males adopted a final copulatory position. With one of the pedipalps under the female, the male raised the female's abdomen, hooked her hind-legs with both pedipalps and slipped under her abdomen in close proximity to the genital opening (Fig. 2d). The male was now hooked to female and he was towed by the female around the mating arena throughout the mating. The male gripped the genital operculum with his mobile cheliceral fingers while the fixed cheliceral fingers were inserted into the female's gonopore.

The process of spermatophore release and transfer was similar for both study species. The male, while still holding the

female, ceased all leg movements, but lifted his abdomen and released onto the ground an amorphous spermatophore from his genital opening. In *Galeodes*, this occurred on average  $95.0 \pm 22.1$  s ( $n = 6$ ) after induction of the immobile state, and in *Gluvia*, it occurred on average  $31.3 \pm 18.7$  s ( $n = 10$ ) from the beginning of the interaction. The male then moved backwards, picked up the spermatophore with his chelicerae, chewed it for a few seconds and thrust it into the genital opening of the female with a series of chewing movements.

In both species, we documented sexual dimorphism in the external morphology of the chelicerae. In *Galeodes*, male chelicerae were straighter than those of females, with the length of the untoothed finger 50% longer in males (Wilcoxon's test,  $P < 0.0001$ , Table 1, Fig. 4a, b). Similarly, *Gluvia* males had straighter chelicerae than females, with the length of the untoothed finger 92% longer in males (Wilcoxon's test,  $P < 0.0001$ , Fig. 4c, d).



**Figure 3** Injuries (marked by arrows) caused during copulation in *Galeodes caspius subfuscus* (a) and in *Gluvia dorsalis* (b, c). (a) Scars on the lateral side of the female propeltidium. (b) Cut-off female hind leg. Note necrosis extending to the trochanter. (c) Broken tips of male chelicera.

After the spermatophore was transferred, the male incorporated it into the female genital opening with intensive rubbing movements. Male *Galeodes* massaged the lower edge of the female's genital opening with lateral movements of his chelicerae. He later changed to more intensive rubbing movements, in which the dorsal parts of his chelicerae were pressed against the female's genital area. The rubbing and massage lasted  $138.3 \pm 34.2$  s ( $n = 6$ ). Numerous bifurcated spines occur on the dorsal side of the fixed finger of a male's chelicerae but are absent in females (Fig. 4a, b). Subsequently, the male closed the female genital opening. Using two cheliceral fingers and flagella, he gripped the soft cuticle of the female's abdomen and pulled it towards the operculum. During this phase, the male was tapping and stroking the female's body intensively with his pedipalps.

Following spermatophore transfer, *Gluvia* males held the female in the copulatory position for  $52.2 \pm 23.7$  s ( $n = 10$ ). With both of his fixed cheliceral fingers deeply inserted, he rubbed the female genital opening intensively, thereby vibrating the female's abdomen. Females stopped moving and both individuals ceased all other body movements for  $31.0 \pm 9.4$  s ( $n = 11$ ). The male then closed the genital opening. Females struggled to free themselves by kicking and/or curving the propeltidium during most of the mating interactions (82%,  $n = 11$ ). In one case, the fixed fingers of the male's chelicerae were broken off (Fig. 3c) as a consequence of struggling. Neither tapping nor stroking of the female's body occurred.

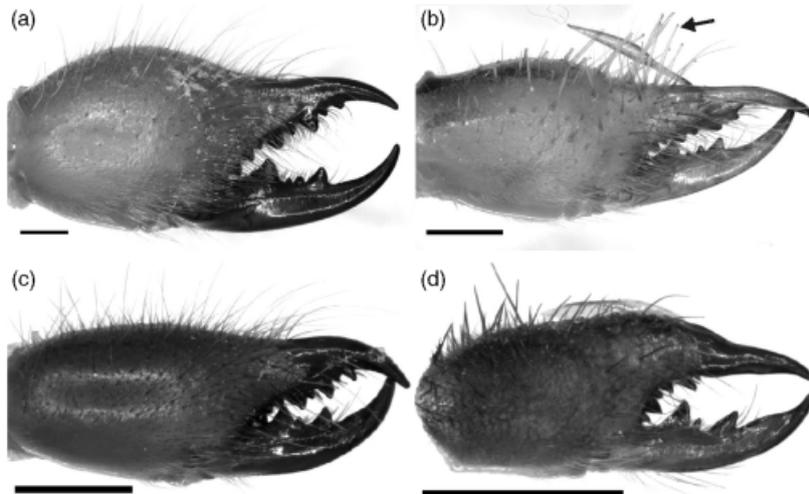
*Galeodes* females never struggled to free themselves following induction of the immobile state. In contrast, *Gluvia* females struggled in most cases (75%,  $n = 20$ ) and succeeded in dislodging the male and interrupting mating in 46.7% ( $n = 15$ ) of the trials. The mean duration of the entire mating interactions in *Galeodes* was  $238.1 \pm 61.3$  s ( $n = 6$ ), and in *Gluvia*, it was  $91.1 \pm 10.2$  s ( $n = 11$ ).

## Discussion

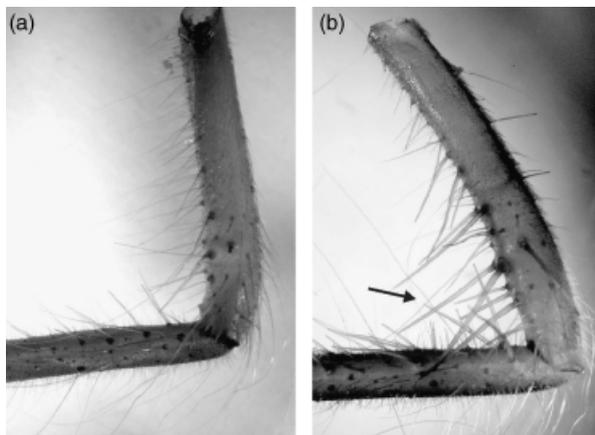
The results here show that mating behaviours differed markedly between the two camel-spider species. However, in both species, several important behavioural features clearly demonstrate coercive copulation: (1) males used superior strength or fast movement to grab the female; (2) males prevented female counter-attack by locking her body and extremities during interaction; (3) males injured females during copulation; (4) females struggled to interrupt the mating (*G. dorsalis* only). Coercively mating *Galeodes* males performed luring behaviour as well, consisting of courtship before copulation (soft stroking and tapping with pedipalps) and during copulation (extensive stroking and tapping with pedipalps, copulatory courtship). The occurrence of pre-copulatory courtship in coercively mating males has not been reported. In *Gluvia*, forced copulation was the exclusive mating strategy.

## Coercive traits

Males of both species used strength or fast movement to grab the female. This trait is typical for intersexual



**Figure 4** Chelicera of *Galeodes caspius subfuscus* (a, b) and *Gluvia dorsalis* (c, d). (a) Female chelicera. (b) Male chelicera. Arrow points to bifurcated spines. (c) Female chelicera. (d) Male chelicera. Scale bars = 2 mm.



**Figure 5** Ventral spines (arrow) on pedipalpal femora and tibia in the female (a) and male (b) of *Galeodes caspius subfuscus*.

interactions in which males force females to copulate (Clutton-Brock & Parker, 1995). In *Galeodes*, the male approached the female frontally and used the suctorial organ to perform a peculiar acrobatic jump over the female's chelicerae. In contrast, *Gluvia* males avoided frontal encounters and assaulted the female from the side or from the rear. Similar grasping of the female has been described in other camel-spiders: eremobatids (Muma, 1966), solpugids (Wharton, 1987) and ammotrechids (Peretti & Willemart, 2007). Comparable coercive tactics also occur in coercively mating bush crickets (Vahed, 2002) and water striders (Arnqvist & Rowe, 1995).

If males evolved adaptive traits to grab the female and enforce copulation, we would expect to find sexual dimorphism in the relevant morphological traits. Indeed, we found significantly longer pedipalps in *Galeodes* males that secure a safe distance while they jump across the female's chelicerae. *Gluvia* males pursued females quickly, and their rearmost legs as the main locomotory legs were significantly longer than those of females, indicating that they can run faster.

In both species, the initial action of a male was to grab the female laterally, by which the male physically restrained the female from counter-attack or escape. This posture has been observed in most camel-spider species (Junqua, 1966; Muma, 1966; Wharton, 1987; Peretti & Willemart, 2007). The manner in which camel-spider females are grabbed by males resembles a typical predatory attack. Interestingly, males were captured in a very similar way by cannibalistic females.

To hold the female *in copula* and to avoid her attack, males either induced an immobile state in the female (*Galeodes*) or hooked her body from behind (*Gluvia*). The induction of the immobile state was reported previously in galeodids. In agreement with previous studies (Junqua, 1966), the immobile state arose only after a mechanical stimulus – the male skewered and squeezed a female's propeltidium in his chelicerae. Determining whether the immobile state was induced by force or adopted by female as a way to allow the male to copulate is difficult. Because Heymons (1902) was able to induce immobilization by squeezing the female propeltidium with a pincer, active induction of immobilization by the male may occur. Indeed, the induction of the immobile state seemed to be caused by the male when clasping the female. However, females could adopt the immobile state once the male released his clasp as a co-evolutionary adaptation to avoid injury under coercive matings.

In *Gluvia*, no induction of immobilization or other form of submissive posture occurred. Instead, the male restricted the female's mobility by hooking her rearmost legs and holding onto their surface with his legs. Similar behaviour has been observed in camel-spiders of the families Eremobatidae (Muma, 1966) and Ammotrechidae (Peretti & Willemart, 2007). These authors hypothesized that the rearmost legs are clasped to limit female locomotion, as locked females moved slowly and with difficulty. We further suggest that such behaviour prevents females from escaping copulation and from attacking the male.

During copulation, a *Galeodes* male would clasp the female's body with his spiny pedipalps. Similar clasping of the female might take place in other galeodid species (Junqua, 1966) as males possess similar pedipalpal spines. Interestingly, no spines occur on the pedipalps of *Gluvia* for which males do not perform clasping of the female body. Thus, spines may be morphological adaptations that function as copulatory claspers.

Forced copulation can result in serious damage to females (Crudginton & Siva-Jothy, 2000; Vahed, 2002). We found such damage in mated females of both species. In all *Galeodes*, varying levels of cuticular damage on the propeltidium occurred in all females, but only a proportion of *Gluvia* females' extremities were seriously damaged. Of females collected in the field in previous years, 20.5% ( $n = 44$ ) had necroses on leg segments possibly caused by coercive males. This frequency of damage caused by coercive mating corresponds closely to that observed in this study. Interestingly, in *Gluvia*, the male's chelicerae (an intromittent organ) was broken in a single case after spermatophore transfer. This phenomenon has not been reported previously for camel-spiders and is probably rare as we did not find such damage in field-collected *Gluvia* males ( $n = 80$ ). The presence of cuticular damage was reported in female camel-spiders of coercively mating ammotrechids (Peretti & Willemart, 2007) and was caused by male pedipalpal spines.

Previously mated *Gluvia* females chased away or killed all subsequent males that attempted to mate, and re-mating was only completed in two cases. Interestingly, re-mating was more common in *Galeodes* and in other galeodids (Amitai *et al.*, 1962; Junqua, 1966) that possess the immobile state. Perhaps serious copulatory damage, such as that found in *Gluvia*, prevents females from re-mating (Johnstone & Keller, 2000).

Females resist forced copulation in virtually all coercively mating species (Thornhill, 1980). In *Gluvia*, all females struggled by kicking and turning the propeltidium, which resulted in interruption of one-third of all mating attempts. Similar behaviour occurs in an ammotrechid, for which vigorous shaking by females resulted in interruption of mating in half the trials (Peretti & Willemart, 2007). In other arthropods, such as water striders and bean weevils, females succeeded in dislodging males by rapid movement, kicking and biting (e.g. Arnqvist & Rowe, 1995). Such resistance did not occur in *Galeodes*, in which the immobile state was induced in the female.

Female resistance might have different functions in different taxa. In sepsid flies, female resistance may communicate lack of receptivity (Baena & Eberhard, 2007), whereas in coelipod flies, it is used for physical dislodgement of males (Crean & Gilburn, 1998). Our observations are in agreement with the latter function.

### Luring traits

Despite copulation in *Galeodes* being clearly coercive, all males performed two different forms of luring behaviour:

pre-copulatory and copulatory courtship. Although pre-copulatory courtship is widespread in arachnids (Proctor, 1998), it is rare in camel-spiders. Pre-copulatory courtship has been observed only in two camel-spider species (Wharton, 1987; Peretti & Willemart, 2007).

Copulatory courtship in the form of stroking, tapping, rubbing and vibrating the female or chewing the female's genitals with the chelicerae when the spermatophore has been transferred occurs in many arachnid and insect species (Eberhard, 1996; Holland & Rice, 1997). We recognized this behaviour in both species but mainly in *Galeodes*. In *Gluvia*, only the intensive rubbing movements of the male's chelicerae inside the female's genital opening were observed. This behaviour occurred immediately after spermatophore insertion, and so it might relate to the mechanics of insemination (Shuker *et al.*, 2002) rather than to sexual stimulation.

### Male mating strategies under the risk of cannibalism

Female *Gluvia* and *Galeodes* are highly cannibalistic, suggesting that coercive mating strategies have evolved to avoid cannibalism. Possibly some of the male coercive traits are assessed by females to choose superior males. Female resistance to mating would then function to evaluate male quality. The fact that females are injured during forced copulations, however, makes this explanation less likely.

Here, we have documented two distinct mating strategies used by camel-spiders: pre-copulatory courtship, combined with an immobile state, and a purely coercive strategy. Thus, courtship and forced copulation are not mutually exclusive mating strategies (Vahed, 2002; Peretti & Willemart, 2007), and pre-copulatory courtship can precede forced copulation. Interestingly, males were able to re-mate only in the species where females were paralysed in the immobile state. If immobilization is induced by males, this trait may lead females to re-mate at suboptimal rates as a result of intersexual conflict over the mating rate (Chapman *et al.*, 2003). Coercive mating may therefore function both to reduce the risk of sexual cannibalism and to increase male mating success with resistant females.

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## Supplementary Information

Additional Supporting Information may be found in the online version of this article:

**Video S1.** Courtship and copulation in *Galeodes caspius subfuscus*. The footage has been shortened markedly to show only the most important events.

**Video S2.** Mating in *Gluvia dorsalis*. The footage has been shortened slightly to show only the most important events.

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