Mating behaviour of *Eremobates pallipes* (Say, 1823) (Arachnida: Solifugae: Eremobatidae)

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Abstract

Little is known about the reproductive behaviour of solifuges, or camel spiders (Arachnida: Solifugae). Behavioural research is limited, due in part to challenges of maintaining specimens in the laboratory where they can be best observed. The present study documents the courtship and mating behaviours of a North American solifuge, *Eremobates pallipes* (Say, 1823) through staged mating encounters in an arena within a laboratory setting. Trials were filmed and analysed to establish sequence and timing of behaviours. We were able to document consistent and predictable aspects of the mating behaviours in this species. The consistent use by males of the suctorial organs during mating was documented for the first time in Eremobatidae.

Keywords: Camel spiders • courtship • reproduction • suctorial organ • wind scorpions

Introduction

Little is known about the reproductive biology of solifuges, or camel spiders, primarily because of challenges inherent in maintaining laboratory populations. Solifuges are notoriously difficult to keep alive in the laboratory for extended periods. Limited investigations of mating have been conducted for only a few genera in five of the twelve families: Ammotrechidae, Daesiidae, Galeodidae, Eremobatidae, and Solpugidae (Heymons 1902; Amitai, Levy & Shulov 1962; Junqua 1962, 1966; Cloudsley-Thompson 1961, 1967a, 1967b; Muma 1966; Wharton 1987; Punzo 1998a; Peretti & Willemart 2007; Hruškova-Martišová, Pekár & Gromov 2008; Hruškova-Martišová, Pekár & Bilde 2010). Many accounts of courtship and mating interactions are from a single, serendipitous observation.

In those species in which copulation has been observed, males typically use their chelicerae to clasp and knead the genital area of the female during the initial courtship stages and again following sperm transfer (Amitai, Levy & Shulov 1962; Muma 1966; Wharton 1987; Punzo 1997, 1998a, 1998b; Peretti & Willemart 2007). Males possess a specialized structure on each cheliceral fixed finger called a flagellum (or flagellar process in Eremobatidae) whose function is unknown but is likely to be involved in sperm transfer (Beccaloni 2009; Bird, Wharton & Prendini 2015). The behavioural sequences involved in courtship and copulation in solifuges and the functional significance of the cheliceral morphology are poorly understood.

The purpose of the present study was to document the mating behaviour of *Eremobates pallipes* (Say, 1823) (Eremobatidae) and compare the observed behavioural sequence with those previously documented for other species in the family. Muma (1966) staged mating trials for three species of Eremobatidae: *Eremobates durangonus* Roewer, 1934, *E. palpisetulosus* Fichter, 1941, and *E. nodularis* Muma, 1951. Punzo (1997, 1998b) recorded some details about the mating behaviours involved in *E. palpisetulosus* and E. *marathoni* Muma, 1951. In Muma's (1966) study, successful matings were few in that only six out of 34 (18%) were complete, and most pairings resulted in rejection. (Rejections included multiple contacts and the retreat of one or both sexes or the receipt of an injury to either individual). Although times spent on specific behaviours varied between species, overall similarities in mating behaviour of the three species were enough that Muma assumed all species of *Eremobates* exhibit the same basic mating behaviours (Muma 1966: 346–347). He divided the stages of mating into the "attack phase" (the actions of the male and female prior to the sperm transfer process), the "contact phase" (the actions of the pair during the transfer process) and the "release phase" (their actions post-sperm transfer).

Typically during the attack phase, one or both individuals assume an aggressive stance: chelicerae open, pedipalps and first pair of legs raised and a rocking motion of the body on Legs II–IV. Actual aggression or combat occasionally occurs in the initial contact phase but, more commonly, either individual may retreat at this point. If the female backs away, the male will commonly spring towards her and make contact with her body. It is also common, especially in *E. palpisetulosus*, for the female to show submission by lowering her body to the substrate as she relaxes her legs, closes her chelicerae, and assumes a back-bend position with her peltidia over her abdomen. If this does not take place, the male may give chase to the female and grasp her in his chelicerae; in Muma's studies this approach resulted only in incomplete mating. Whether contact is established through male aggression or female submission, the contact phase progresses much the same.

The second or contact phase of mating is characterized by the male's palpations of the female's body with his chelicerae, usually at the meso- and metapeltidium, working his way to her genital region. In *E. nodularis* the male immediately initiated chewing at the genital opening. This genital-chewing action by the male appeared to stimulate the female to enter a quiescent state such that the male was able to manipulate her body easily, turning her onto her side or back. Then he inserted the fixed fingers of his chelicerae into her genital opening (Muma 1966). From this position the male maneuvered the female into an overhead, forward-facing stance. At this stage, he began rough chewing or kneading her genital area and, if she was less quiescent or attempted to escape, he jerked her body or lifted and carried her (Muma 1966). Throughout this, his fixed fingers remained inserted in her genital opening and he used his

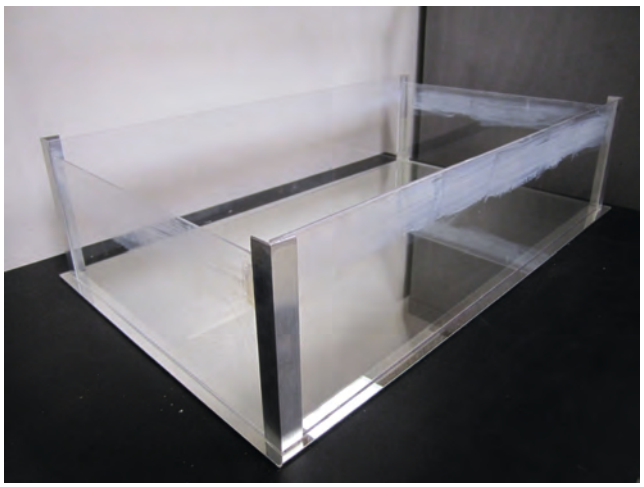

Fig. 1: The mating arena with acrylic walls and a mirrored floor. Wall dimensions are 62 cm long × 36 cm wide × 14 cm high.

pedipalps and first pair of legs to stroke her peltidia and legs in a forward direction, and her abdomen in an upward motion. This portion of the contact phase maintained (or achieved if she was not initially willing) the female's quiescence.

Immediately prior to sperm transfer the male removed his chelicerae from the female's genital opening and forcibly manipulated her body so that her abdomen was positioned further over her peltidia. In *E. durangonus*, *E. palpisetulosus*, and *E. nodularis*, transfer of the sperm droplet occurred in 1–2 seconds, directly from the male genital opening onto that of the female (Muma 1966). *Eremobates durangonus* and *E. palpisetulosus* males held mates around the abdomen with their pedipalps during transfer, an action thought to guarantee successful delivery by ensuring the restraint of the female. Following transfer, the male moved behind the female and again inserted his cheliceral fixed fingers into her genital opening and chewed more slowly than pre-transfer genital kneading (Muma 1966). Muma suggested that this action served either to force sperm into a storage area within the female or to break open the membrane of the sperm packet and introduce the sperm into the female. Throughout this secondary chewing the male stroked the female until she resumed activity and usually fled.

The third and final eremobatid mating phase described by Muma (1966) is the release phase. Behaviours ranged from continued post-release quiescence of the female while the male rested nearby and engaged in a chewing motion (possibly to clean any traces of sperm from his chelicerae), to the flight of both sexes. The pair also sometimes entered into direct combat. Occasionally, sexual cannibalism resulted (Cloudsley-Thompson 1961; Punzo 1997, 1998b). Rarely males ate females (Muma 1966). Death of the male or female was more common in *E. palpisetulosus* than in *E. nodularis* or *E. durangonus* (Muma 1966).

In *E. durangonus*, mating times ranged from 4–17 minutes; *E. palpisetulosus* matings took 8–9 minutes (Muma 1966). As most incomplete matings in Muma's 1966 laboratory trials ceased after the initial genital chewing, it is thought that the males might be encountering seminal fluid within the female from previous matings; in one case a droplet of fluid was actually observed on the chelicerae of the male as he withdrew.

The objective of the present study was to obtain data on the courtship and mating interactions of *Eremobates pallipes* (Say, 1823) in a laboratory setting, such that interactions could be readily staged and filmed. By doing so, we could then compare the behavioural sequence in this species with those previously documented by Muma (1966).

Methods

All *Eremobates pallipes* specimens used in these trials were collected from Caprock Canyons State Park in Texas (34.410639°N 101.054824°W). All mating trials took place within an open-topped, clear acrylic glass arena (Fig. 1). The bottom consisted of a mirror, to allow for ease of observation and recording of copulatory behaviours from various angles. The dimensions of the acrylic glass walls were 62 cm long, 36 cm wide and 14 cm high. INSECT-a-SLIP® (available from BioQuip Products, Inc.) was applied to the top 5 cm of the inside wall to prevent escape by climbing during trials. Following each arena occupancy, the mirror and walls were cleaned with hot water; to avoid possible irritation of the animals, no other chemical cleaning products were used. All mating encounters were filmed with a Nikon D90 DSLR. All footage was reviewed to ascertain the duration and sequence of behaviours and to determine if any sequential deviances occurred. Times are reported in seconds (sec).

Sufficient males were collected (n = 13) such that each male could be used once, although three (CC-59, CC-73, and CC-75) were introduced to more than one female (see Table 1). Six of the males moulted to maturity in the laboratory (see Table 1; males denoted by *). These were the only males whose virgin status was ensured. The mating status of all other wild-caught males used during the trials was unknown. Fewer adult females were collected in the field, which is not uncommon for these arachnids (PEC, personal observation); mortality rate of females that were collected was also high. Thus, we only had n = 8 females available for use in the trials and, therefore, each was used in more than one pairing. Three females matured in the laboratory and were, therefore, virgins when first introduced to males (see Table 1; females also denoted by *). The mating status of all other wild-caught females was unknown.

Primary housing enclosures were large, glass mason jars with a dirt substrate and some loosely-crumpled paper toweling resting on the substrate. Prior to initiation of a mating trial, both male and female specimens intended for pairing were removed from their housing enclosures into 40 dram plastic vials. This step was taken to allow the animals to settle after removal from enclosures (Muma 1966) and to control timing of the animal's introduction to the enclosure. Female specimens were always first to be introduced to the mating arena and were placed in a central location. If the

female was active and began to explore her surroundings, she was allowed five solitary minutes prior to introduction of the male; if she remained stationary in the location of her introduction or if she ceased movement, she was allowed two solitary minutes prior to male introduction. The male would be placed in the arena as far as possible from the female, usually in a corner opposite her position. If the pair did not a) seek each other out or b) did not encounter one another within five minutes, they would be segregated into vials once again. If non-violent rejections occurred (see below), the pair were separated but still considered for alternate pairing with a different partner. If the rejection by one or both individuals was violent, care would be taken to immediately segregate them. Separation was attempted in hope of avoiding any female injury due to the paucity of adult females. In some cases of violent rejection or mating culminating in violence during which males were killed by the female; care was still taken to retrieve the male without causing harm to the female, such that the remains of the deceased male could be preserved in the best state possible (voucher specimens from these trials were deposited in the arachnology collection at the Denver Museum of Nature & Science).

Females used more than once in mating trials were never used on the same day if they had accepted a male. No repeat pairings of males and females that had been previously together were staged, regardless of the outcomes of those pairings (accepted or rejected, successful or unsuccessful).

Successful matings began with the acceptance by the female, indicated by her entrance into a quiescent state, or a state of torpor, upon being contacted by the male. Rejections were initiated by either sex or were mutual. Instances of mutual rejection were characterized by both male and female exhibiting rejecting behaviour. Violent rejections were aggressive agonistic responses, indicated by defensive postures, lunging behaviour and/or attempts to bite. In non-violent rejections one or both individuals retreated. For example, a non-violent mutual rejection could be one in which both male and female recoiled from contact with one another (a sudden lurch backward, still oriented towards one another), or when both simply turned and fled. Overall times of interactions culminating in rejection were not included in the results as these exchanges did not progress to their natural conclusion; intervention occurred to prevent possible cannibalism.

Matings were considered successful and complete if the female became quiescent upon contact by a male, and if he proceeded through a sequence of mating behaviours culminating in gonopore to gonopore (GO-GO) contact. If gonopore contact was not observed prior to releasing the female, the mating was considered unsuccessful or incomplete. As sperm transfer was not readily visible, in all cases of disengaging after GO-GO contact it was assumed that sperm transfer had transpired. Matings were also considered unsuccessful if the male did not achieve cheliceral kneading of the female's genital operculum, or if the female emerged from her quiescent state prior to the observation of an apparent sperm transfer. Muma's stages of mating in *Eremobates* were used as the framework for comparison: the attack phase, the contact phase, and the release phase (Muma 1966).

Results

The overall setup of the arena proved very effective in allowing careful observation of the sequences of behaviours consistent with eremobatid mating. The wide, open-topped arena easily facilitated recording the behaviours. The mirror allowed for observation of the underside of the pair. The application of the INSECT-a-SLIP® along the inside edges of the arena prevented solifuges from climbing out.

Tallarovic, Melville & Brownell (2000) reported some difficulty maneuvering in scorpions when staged in mating

Date	Trial	♂ #	♂ experience	♀ #	♀ experience	Outcome
22 Aug 2012	1	CC-21	1st	CC-22	1st	A/U
23 Aug 2012	2	CC-12	1st	CC-22	2nd	A/U
27 Aug 2012	3	CC-24	1st	CC-22	3rd	A/U
13 Aug 2013	4	CC-91	1st	CC-93	1st	A/U
13 Aug 2013	5	CC-90	1st	CC-95	1st	A/U
14 Aug 2013	6	CC-85	1st	CC-93	2nd	A/S
14 Aug 2013	7	CC-76	1st	CC-95	2nd	R/V/U
14 Aug 2013	8	CC-81	1st	CC-95	3rd	A/S
15 Aug 2013	9	CC-86	1st	CC-80	1st	A/S
25 Aug 2013	10	CC-59*	1st	CC-49*	1st	A/S
25 Aug 2013	11	CC-71*	1st	CC-80	2nd	A/S
25 Aug 2013	12	CC-66*	1st	CC-65*	1st	A/S
25 Aug 2013	13	CC-75*	1st	CC-93	3rd	R/NV/U
25 Aug 2013	14	CC-75*	2nd	CC-95	4th	R/V/U
25 Aug 2013	15	CC-73*	1st	CC-95	5th	R/NV/U
25 Aug 2013	16	CC-73*	2nd	CC-93	4th	R/NV/U
06 Sep 2013	17	CC-59*	2nd	CC-61*	1st	R/NV/U
06 Sep 2013	18	CC-59*	3rd	CC-65*	2nd	A/S
06 Sep 2013	19	CC-67*	1st	CC-93	5th	A/S
08 Sep 2013	20	CC-98	1st	CC-99	1st	R/NV/U

Table 1: Specimens used in *Eremobates pallipes* mating trials in this study, the animal's experience (1st mating, 2nd mating, etc.) and overall outcomes of each trial, n = 20. A = accepted, R = rejected; type of rejection: V = violent, NV = non-violent; M = rejection by male, F = rejection by female; final outcome: S = successful, U = unsuccessful; * = maturity reached in captivity.

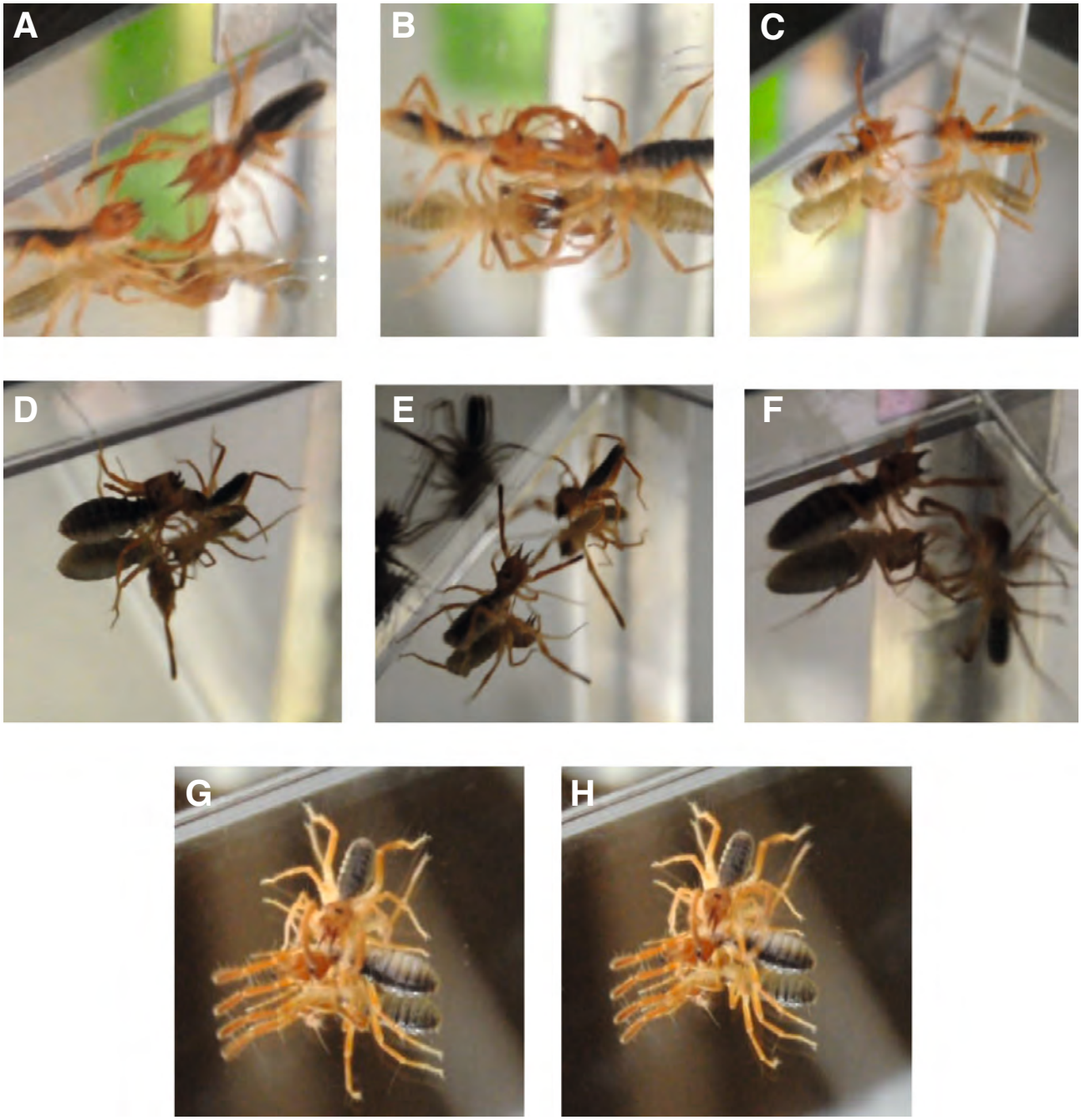

Fig. 2: Initial encounters during *Eremobates pallipes* trials. **A** violent rejection by female (right); **B** mutual violent rejection (male on left, female on right); **C** a non-violent rejection (female on left, male on right); **D–F** initial contact with the pedipalps (female on left); **G–H** initial contact from the side. Females are in the quiescent state in D, G, and H. All trials were staged on a mirrored surface.

Behaviour	Code	Description of Behaviour
First Contact	FC	First contact of male with female. Contact can be with chelicerae or pedipalps. Results in immediate quiescence of female and cessation of her movement. Female's body is bent at nearly right angle, exposing her gonopore.
Chelicerae Near Operculum	CNO	Movements of male chelicerae near female's gonopore (pre-insertion).
Insertion-Chewing & Palpal Stimulation	I/C & PS	Male inserts fixed finger of chelicerae into female's gonopore and chews while he stimulates her with palps and 1st legs.
Withdrawal, Gonopore Contact, and Sperm Transfer	GO-GO	Male quickly withdraws his chelicerae, moves his body up and makes direct gonopore to gonopore contact. Sperm packet deposited at female's opening.
Reinsertion	RI	Male reinserts cheliceral fixed finger.
2o Chewing	2o C	Male commences chewing motion with fixed finger of chelicerae, presumably pushing sperm into female and releasing sperm (may also remove competing male's sperm).
Suctorial Holding	SH	Male uses suctorial organs at distal end of pedipalp to hold onto female and rock her body.
Female Revives	FR	Female's jaws and legs begin to twitch as she emerges from the quiescent stage.
Female Struggle	FS	Female begins to struggle.
Female Intense Struggle	FIS	Apparent intense struggling by female to escape from the male.
Male Release	MR	Male releases female and both retreat.

Table 2: Ethogram of behaviours and behavioural sequences during successful matings of *Eremobates pallipes*.

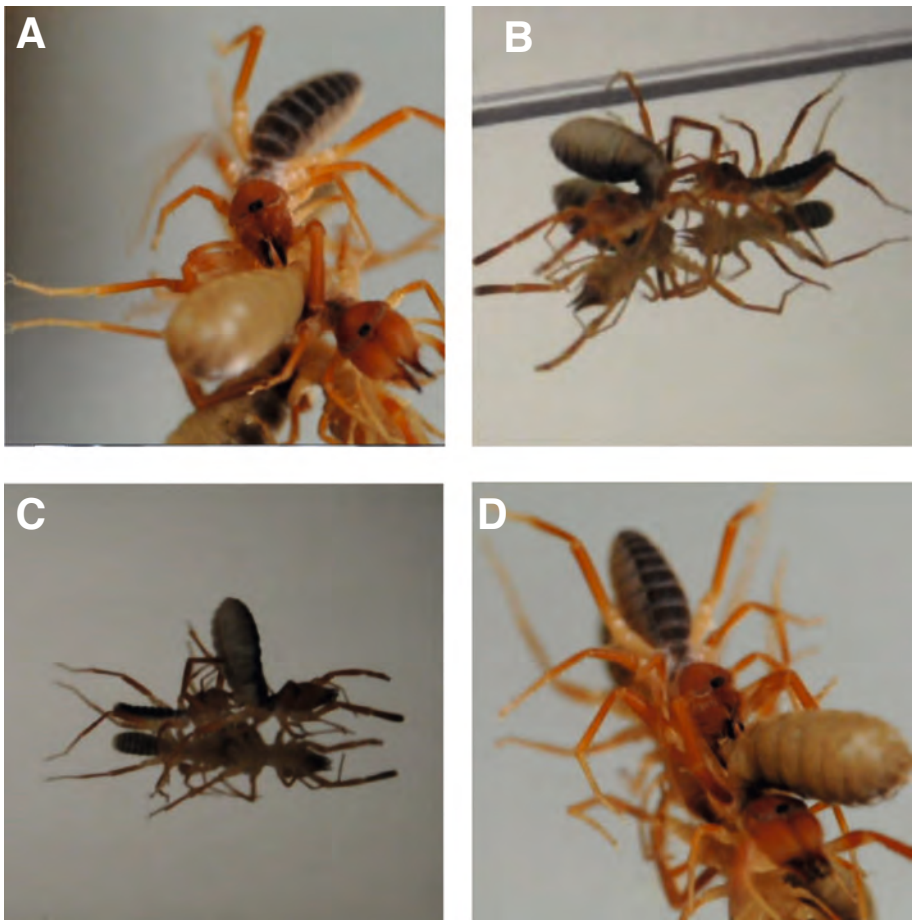

Fig. 3: Mating stages of *Eremobates pallipes*. **A–B** pre-insertion fixed finger movements in the female's genital region; **C–D** the first insertion and simultaneous palpal stimulation.

trials on a glass surface; for the most part, this did not appear to be an issue for the solifuges. In a few instances a female's progress and movement would be slowed if her abdomen was particularly large as noted by Punzo (1998c). Mature females have fully developed eggs visible beneath the cuticle of the abdomen regardless of their mating status (Junqua 1966). On one occasion a small male was coupled with quite a large female; he appeared to have some difficulty maneuvering her (and at several points the pair fell over, though this did not deter him in the least) but likely this would have been the case regardless of the mating surface.

All mating stages are illustrated in Figs. 2–6, still images taken from videos of the mating sequence. An ethogram of the behaviours involved in E. pallipes mating is presented in Table 2. Table 3 presents times for each behavioural sequence recorded in 13 trials in which males were accepted by females. In E. pallipes, receptive females become quiescent the instant they are contacted by the males (Table 2). Quiescence (FC, Tables 2 and 3) was achieved regardless of the angle of approach by the male. In one case a female approached a male from behind: the instant that her pedipalps came into contact with him he turned 180° to touch the female with his pedipalps, at which time she instantly entered the quiescent state. With both fixed fingers inserted (I/C in Tables 2 and 3), males engaged in a chewing behaviour that involved both a forwards and backwards motion of the chelicerae as well as opening and closing of the moveable fingers. Chewing always began immediately upon insertion of the fixed finger of the chelicera and was simultaneous with the onset of the male's pedipalps supporting the female's abdomen (PS in Tables 2 and 3). The male would accomplish this by a combination of wrapping his pedipalps around her abdomen in a sort of embrace and by keeping his pedipalps raised and outstretched such that they provided support and rocked the female's abdomen side to side between them. The abdomen of the female was pushed directly upwards, or even over her propeltidium (Fig. 3). While chewing, the male also stimulated the female's body with his pedipalps and first legs (I/C & PS in Table 2).

Prior to the brief detachment by the male to achieve GO-GO contact and sperm transfer, a juddering behaviour of the male's body was nearly always observed. This involved a rapid forward and backward vibration of the entire body. During juddering, the male maintained his hold or balancing of the female's forward-thrust abdomen but paused in palpal and 1st leg tapping and stroking. This behaviour consisted of 2–3 judders, 1–4 times leading up to sperm transfer. In one case, juddering began almost immediately following the initial insertion of the fixed fingers and was maintained until withdrawal of the fixed fingers for sperm delivery.

Males rapidly withdrew the cheliceral fixed fingers (Fig. 4A) and immediately pressed their gonopore to that of the female (Figs. 4B–C; GO-GO, Table 2). The time of GO-GO contact was always ≤ 1s (n = 8). Males then re-inserted their

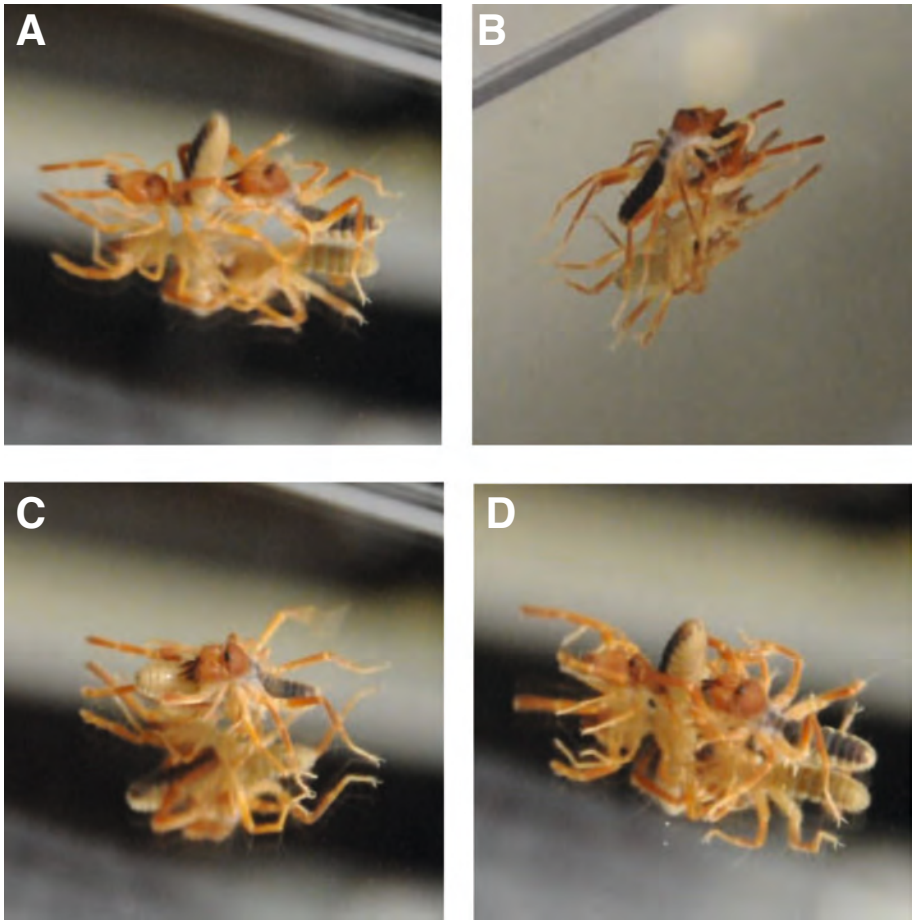

Fig. 4: Mating stages of *Eremobates pallipes*. **A** male withdrawal from cheliceral chewing; **B–C** the male pressing his gonopore to that of the female; **D** reinsertion of the fixed fingers.

fixed fingers into the female's genital opening (Fig. 4D; RI, Tables 2 and 3) and resumed the chewing action (secondary chewing stage, or 2o C in Table 2).

A completely novel behaviour for Eremobatidae was noted in all successful *E. pallipes* trials (n = 8), as well as some of the unsuccessful trials (see Tables 2–4). This behaviour normally occurred following the reinsertion of the fixed fingers after GO-GO and the resumption of chewing by the male: males would adhere both suctorial organs to the female, nearly always to her propeltidium and regu-

Trial	FC	CNO	I/C & PS	Overall Time (up to 1st release)	RI	2o chewing	SH	Time of ♀ revival	Time: transfer to revival	Time: SH to revival	♀ struggle	♀ intense struggle	Male Release (Overall time)
1*	1:32	0:11	0:38				0:04				0:11		2:23
2*	0:09	0:30	0:01								0:06		0:47
3*	0:04							1:20					1:20
4*	0:06	0:14	3:07	3:28	0:12	1:01	0:39	4:13	0:45		0:29	0:10	4:42
5*	0:06	0:10	1:49	1:05	0:08	1:37	1:46	3:24	2:19	0:35	0:34	0:12	4:13
6	0:06	0:15	6:08	6:24	0:05	1:34	1:07	6:49	0:36	-0.06**	0:57	0:02	8:04
8	0:02	0:01	3:21	3:24	0:06	2:26	2:16	4:30	1:06	0:47	0:15	1:22	5:59
9	0:06	0:15	4:40	4:01	0:07	1:40	1:27	5:32	1:31	0:09	0:46	0:00	6:50
10	0:08	0:03	1:19	1:30	0:06	1:28	1:15	2:04	0:34	0:15	0:18	0:32	2:04
11	0:04	0:16	3:34	4:03	0:09	0:39	0:20	4:26	0:23	0:04	0:04	0:10	4:42
12	0:09	0:02	1:40	1:51	0:05	1:31	1:16	2:13	0:22	0:02	0:07	0:00	3:27
18	0:17	1:15	1:39	3:02	0:12	0:32	0:15	3:33	0:31	0:01	0:03	0:06	3:47
19	0:07	0:17	3:01	3:10	0:07	1:25	1:12	4:03	0:55	0:16	0:23	0:18	4:53

Table 3: Times spent on behaviours during mating in *Eremobates pallipes*. Data from trials in which males were accepted are included (n = 13). Trial #s correspond to Table 1. * = trial that was incomplete or contained deviations; ** = female revived prior to the initiation of suctorial holding behaviour; FC = first contact; CNO = chelicerae near operculum (pre-insertion); I/C = insertion/chewing; PS = palpal stimulation; RI = reinsertion; SH = suctorial holding.

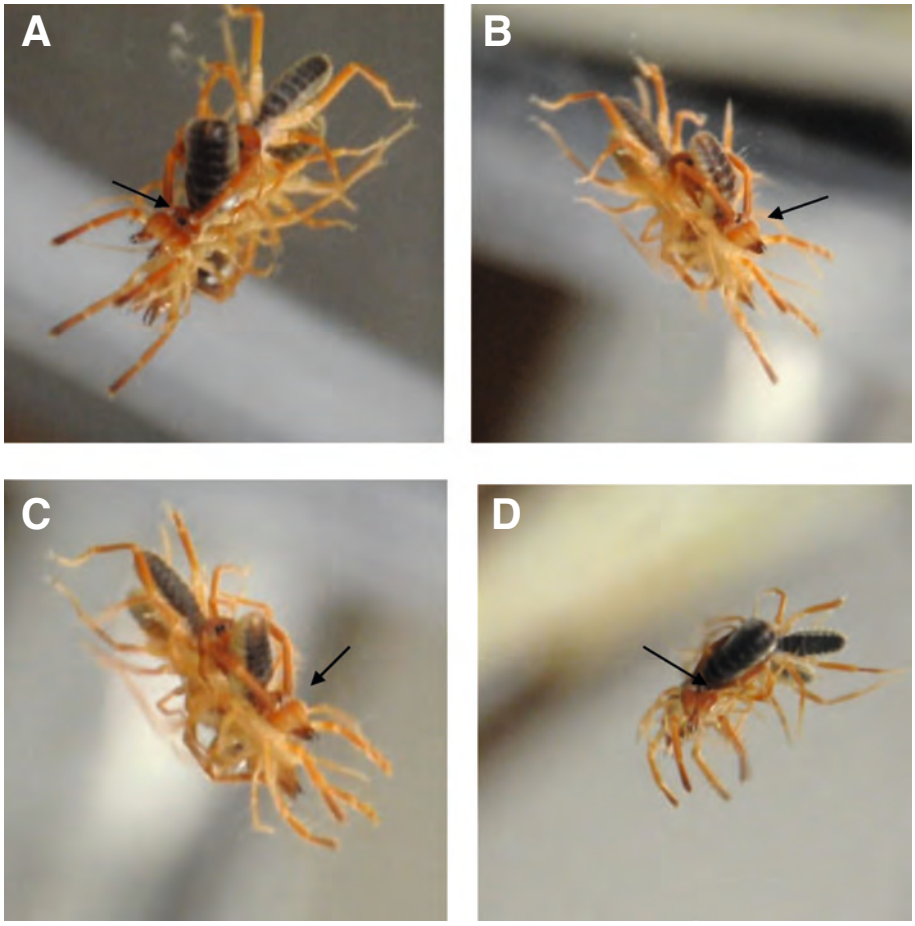

Fig. 5: **A–D** use of the suctorial organs during mating by male *Eremobates pallipes* during the secondary chewing stage. Arrows point to the everted suctorial organs.

larly over the eye region (but occasionally one would end up elsewhere such as the side of her chelicera or some anterior portion of her abdomen) (Fig. 5, arrows point to everted suctorial organs). Males often attached and reattached the suctorial organs to various locations on the female, always focusing on her propeltidium. Suctorial holding behaviour was maintained from the moment initiated (shortly after reinsertion) until the male released the female.

During quiescence, several females were seen to periodically display some slight tapping of the 2nd and 3rd legs as well as occasional, barely perceptible cheliceral movements. These were the only motions by females noted until she emerged from her apparently induced quiescent stage and revived (FR in Table 2). In trials where sperm transfer took place, no female revived prior to the transfer (Table 3). If there was any deviation from the typical pattern of male mating behaviours, females revived out of turn (observed 4 times, n = 13; see Table 3). All females revived after the reinsertion but prior to release by the male with the exception of one female who revived simultaneously with male release (this mating was incomplete). Female revival can be divided into three stages: revival (the return of some movement), struggle (writhing, leg and pedipalp movement, sometimes the use of the suctorial organs to pull herself forward or grab surfaces such as the arena floor and walls) (Fig. 6A), and intense struggle (Fig. 6B). The latter was not always exhibited, but when present this consists of quite violent struggling such as arching the body upwards and downwards (the rapid alternate flexing of the dorsal aspects of the propeltidium and abdomen toward and away from each other) and/or rolling behaviour, coupled with cheliceral gnashing and attempts to bite the male. Female intense struggle had one of two outcomes: her success in seizing the male (this occurred once in the successful trials) such that the mating sequence was immediately halted, or the avoidance of the female's chelicerae by the male, coupled with the maintenance of the suctorial grip until such time as the male released the female and fled. For female revival times, refer to Table 4.

The release by the male at the conclusion of mating in E. pallipes always consisted of a simultaneous withdrawal of the fixed fingers, release of the suctorial organs from the female's propeltidium and hasty backward retreat. This was accomplished by a rapid flinging motion of the male's entire body (Figs. 6 C–D). Males will reverse several body lengths prior to resuming forward locomotion. No male that successfully disengaged was seized or pursued by the female. In no cases did the male eat or show aggression toward the female after completion of mating. Upon release, females were never quiescent, but resumed regular exploratory locomotion.

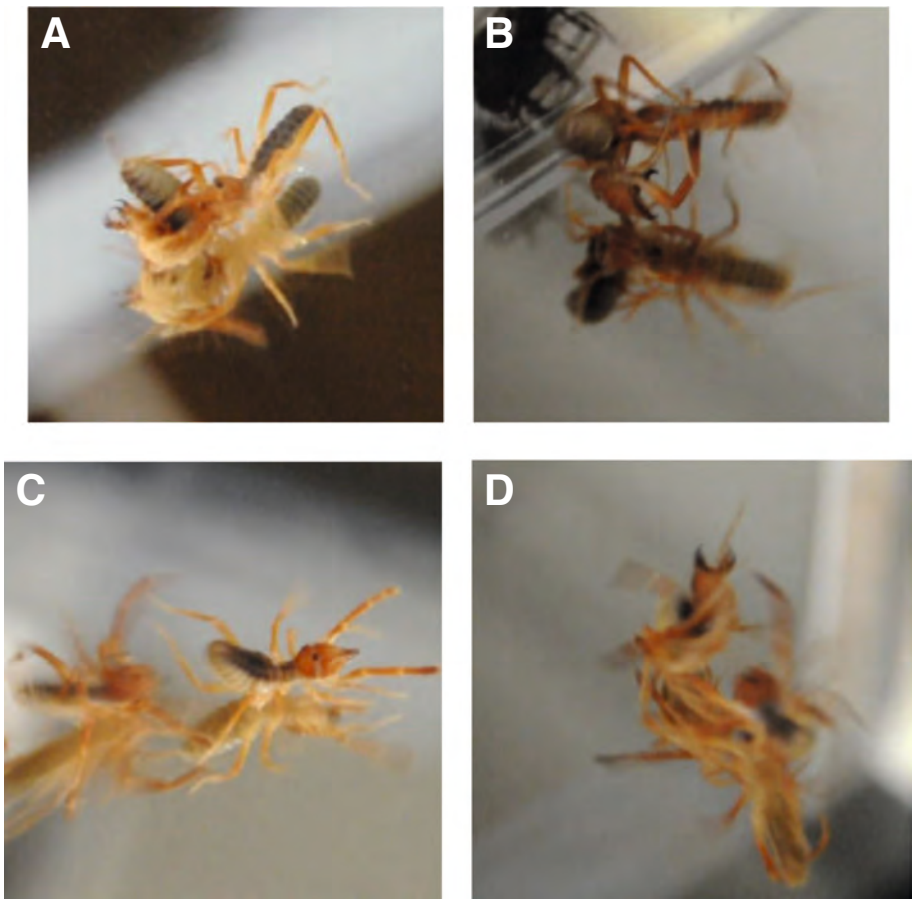

Fig. 6: Mating stages of *Eremobates pallipes*. **A** female struggle (female on left); **B** female intense struggle (female on left); **C–D** male release (C: female on right, D: female above male).

The times spent in each mating behaviour are summarized in Table 3. Of the 20 trials, in 13 the female accepted the male (65%). Of these, eight were successful (40% of trials) (Table 1). Of these eight successful matings, two were between a virgin male and a virgin female (Table 1). The other successful matings were between adult wild caught individuals whose prior mating status was unknown and/or between individuals that had been used in previous mating trials (Table 1). In seven of the trials there was a rejection by one or both individuals. In nonviolent rejections (n = 4): one was a rejection of the female by the male, two were rejections by the female, and the other was mutual. Violent rejections were rare (15% of all trials): two by the female, one by the male. No violent rejections were mutual. The average time ± standard deviation of each behavioural sequence is presented in Table 4 for the eight successful matings.

The only unsuccessful mating trials which began with acceptance by the female (5 of 13 trials in which females initially accepted males; Tables 1 and 3) are those in which some behaviour of the male deviated from the usual sequence or fell well outside of the usual time range for a certain behavioural sequence. In one of these trials, the male spent 1 min 32 sec moving the chelicerae over the female's body prior to focusing his efforts on the genital region; in successful trials, the average time was 7.37 sec (Table 4). In another unsuccessful trial, the male only took 9 sec to locate the female's gonopore, but took 30 sec to insert his fixed fingers; in successful trials, the average time to insertion is 17 sec. The female responded aggressively to this male. In another unsuccessful trial, the sequence progressed as normal until cheliceral insertion. At that time, the male began an almost constant juddering behaviour and did not attempt sperm transfer. In another trial, the male, after being introduced into the arena with the female, ran directly to the female. She became quiescent within 2 sec of his entry into the arena. He then moved his chelicerae over the female for only 2 sec before retreating slightly, holding his pedipalps over her body but not in contact. He maintained this stance and she stayed in her quiescent state for 1 min 18 sec. At that time, she resumed normal activity and the male retreated. More details about mating trials can be found in Rowsell (2014).

Discussion

Muma (1966) described the mating behaviours of *Eremobates durangonus*, *E. palpisetulosus*, and *E. nodularis*; these descriptions were used as a baseline for comparison of *E. pallipes* in the present study. In Muma's (1966) study, only 17% of his mating trails were successful; whereas 40% of our mating trials focused on a single species were successful. The overall time for all behavioural sequences seen as well as the total time for mating in the successful matings was comparable to Muma's findings.

Behaviour	Range (sec)	mean ± SD [only for successful trials] (n = 8)
FC	2–17	7.37 ± 4.47
CNO	1–75	18.00 ± 24.03
I/C & PS	79–368	190.25 ± 99.47
Time to 1st release	90–384	205.62 ± 90.71
RI	5–12	7.12 ± 2.36
2o C	32–146	84.37 ± 35.84
SH	15–136	68.50 ± 38.22
Time to FR	124–409	248.75 ± 95.34
Time from Sperm Transfer to FR	22–91	44.75 ± 24.10
Time SH to FR	-6–47	11.00 ± 16.30
FS	3–57	21.62 ± 19.91
FIS	0–82	18.75 ± 27.77
Time to MR	124–484	298.25 ± 116.34

Table 4: The sequence of mating behaviour for *Eremobates pallipes*. Complete, successful trials only (n = 8). * = one female revived 6 sec prior to the initiation of suctorial holding; FC = first contact; CNO = chelicerae near operculum (pre-insertion); I/C = insertion/chewing; PS = palpal stimulation; RI = reinsertion; SH = suctorial holding.

The behavioural sequences for *E. pallipes* generally corresponded with those described by Muma (1966): the attack, contact, and release phases. In *E. pallipes*, the analog of Muma's attack phase consisted of the male rushing toward the female and grasping her with his chelicerae or pedipalps (FC, Tables 2–4), followed by the immediate cessation of movement by the female (female's quiescence), and the female bending her body over to expose her gonopore. The contact phase in *E. pallipes*, as with Muma's (1966) study, included insertion of and chewing by the male's fixed finger in the female's gonopore (CNO followed by I/C & PS, Tables 2–4) followed by gonopore to gonopore contact (GO-GO, Tables 2–4), sperm deposition, and post-deposition chewing (RI and 2o C, Tables 2–4). Muma's release phase commenced in *E. pallipes* only after the female began to emerge from her state of quiescence.

However, we observed some differences in specific behaviours for *E. pallipes* such as the juddering of the male's body prior to sperm deposition; various stages of female revival (female struggle and female intense struggle, see Fig. 6, Tables 2 and 3); and instantaneous female quiescence (in trials where males were accepted, n = 13). Muma (1966) observed female submission prior to contact by the male (in *E. durangonus* and *E. palpisetulosus* only) or quiescence well after the initial contact. Muma did not mention the role of the pedipalps in the first physical contact; for *E. pallipes*, the pedipalps of one or both individuals are the initial point of contact. It has been suggested that the palpal papillae (modified setae) may have a role in achieving the quiescent response of the female (Cushing *et al*. 2014). In Fig. 3D, the male can be seen to have his pedipalps wrapped around the female's propeltidium; this took place less than 1s after the initial contact. Several previous authors have also reported female quiescence, or torpor, upon contact with the male in: *Eremobates marathoni* (Eremobatidae) (Punzo 1998b); *Galeodes caspius* Birula, 1890 (Galeodidae, Heymons 1902); *Othoes saharae* Panouse, 1960 (Galeodidae, Junqua 1966); *Metasolpuga picta* Kraepelin, 1899 (Solpugidae, Wharton 1987).

It is difficult to say from the data available what triggers either the quiescence (or torpor) or the revival of the female. It could be the reinsertion of the fixed fingers into her genital opening, the adherence of his suctorial organs, or some combination of the above. There could also be some other unrealized cue. Heymons (1902) was able to induce the catatonic stage in the female of *Galeodes caspius* (Galeodidae) using forceps, and Junqua (1966) was able to induce this state in the female of *Othoes saharae* (Galeodidae) with his own fingertips. More research is needed to understand both why the female emerges from her quiescent state as well as what stimuli triggers the onset of this state.

The most novel behaviour recorded was the use by the males of the suctorial organs during mating. The suctorial organs are eversible organs that have previously been reported to be used in prey capture and climbing of smooth surfaces (Cushing *et al*. 2005; Klann *et al*. 2008; Willemart *et al*. 2011). This is the first report of solifuges regularly using suctorial organs during copulation to grasp the female in the Eremobatidae. Male *Galeodes caspius subfuscus* Birula, 1937 were observed employing a single suctorial organ during the attack phase in mating trials conducted by Hrušková-Martišová, Pekár & Bilde (2010). This use of the suctorial organ during mating may be more widespread in the Solifugae. The use of video recordings to document behaviours involved in solifuge matings enabled the observation of suctorial organ use by males. Without video footage that could be reviewed, the involvement of these organs could easily be overlooked. As the sperm transfer in *E. pallipes* is so rapid (≤ 1 sec in all cases) this could easily be missed by observers; review of behavioural sequences by video is highly beneficial.

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