Courtship behaviour of the scorpion, *Euscorpius flavicaudis*

T. G. Benton
Department of Zoology,
University of Cambridge,
Downing Street, Cambridge, CB2 3EJ*

Summary

For the first time the courtship of a scorpion, *Euscorpius flavicaudis* (de Geer) is quantitatively described, based on observations of its courtship both in the field, at Sheerness in Kent, and under semi-natural conditions in a laboratory colony. The courtship lasts about 2 h (range 1–7.5) and involves the male stinging the female. Unlike other reported species of scorpion, the courtship is remarkably uniform; there are no distinct "phases" with apparently different functions. The courtship of this species begins in the female's burrow, and some 85% of the total courtship occurs there. The observations made are discussed in the light of previous studies.

Introduction

Scorpions have always fascinated humans (Cloudsley-Thompson, 1990), and ever since the scorpion's complex courtship "dance" was first reported it has provoked interest. Maccary (1810—quoted in Shulov & Amitai, 1958) described how he saw a male *Buthus occitanus* (Amoreux) attack a female, turn her over and mount her for five minutes. Brongniart & Gaubert (1891) reported that a pair were surprised beneath a rock "accouplés, ventre à ventre". In 1907 (translated into English in 1923) the great French naturalist J. H. Fabre published a popular book on scorpions in which he described the courtship of *B. occitanus*. Fabre expected scorpions to copulate belly to belly and states that he never saw "consummation of the marriage". Little was added to our knowledge of scorpion courtship between 1907 and the mid 1950s. Vachon (1953) stated "anatomical investigation bears out the statements of early writers; the male fertilises the female directly in a true copulation, which is rather rare in other arachnids. In the course of this act, the male protrudes certain special organs to form a temporary penis, with which he inserts the sperm . . ." (page 88). It was not until 1955/6 that descriptions of complete courtships appeared in the literature, and it became apparent that Vachon's "temporary penis" was in fact a chitinous spermatophore by which indirect sperm transfer occurred (Alexander, 1956; Angermann, 1955; Bücherl, 1956; De Zolessi, 1956).

Between the mid-1950s and the present day, the courtship of about 25 species of scorpion has been described in the literature. The courtship is complex and variable and can be very long: up to 24 (Auber-Thomay, 1974) or even 36 hours (Baerg, 1954). However, by far the majority of descriptions have been based on a few individual courtships observed under highly unnatural conditions in the laboratory; and the observations themselves are often of an anecdotal nature. The purpose of this paper is to describe quantitatively the courtship of a scorpion observed in such a way that it is known to be behaving naturally.

*Present address: School of Environmental Sciences, University of East Anglia, Norwich, NR4 7TJ.

Methods

The scorpion used in this study, *Euscorpius flavicaudis* (De Geer), lives in a large, well-established colony at Sheerness, Kent (Benton, 1992a). In Sheerness Docks, where I studied the scorpions for 18 months, they inhabited cracks in the old Dockyard perimeter wall where the cement has crumbled from between bricks. To allow more convenient investigation of aspects of their behaviour, a large laboratory colony was set up, modelled on the habitat at Sheerness. This consisted of a sandpaper-covered plywood wall, with 144 "cracks" built into it. On to this wall were released freshly caught scorpions from Sheerness, and these were allowed to wander freely on the wall. The wall was kept under natural photoperiod, and as near natural temperature and humidity as possible. Each week, woodlice (the scorpion's main food) were released at the base of the wall, from where they ascended at night and were caught by foraging scorpions. Observations of the scorpions' behaviour were conducted at night, for a period of 6 weeks around their mating season.

Scorpions at Sheerness were observed with the aid of ultra-violet light. In the laboratory the scorpions were observed using lamps fitted with deep red filters, which the scorpions cannot see (Machan, 1968).

For details of field-methods see Benton (1992a). For details of the colony see Benton (1991a).

Behavioural sequences were either transcribed directly, with timings, or were dictated into a hand-held tape recorder, from which they were later transcribed. The sequences of behaviours were then cast into transition matrices, which allowed the construction of a behavioural flow-diagram.

In the results, means are given with their associated standard error.

Results

In total, 18 courtships were observed in a state sufficiently complete for analysis (8 field, 10 laboratory). To compare the behaviours in laboratory and field, repeated Measures ANOVA was conducted on a set of 13 parameters of the courtship (such as length, numbers of certain behaviours, etc). The analysis showed that, overall, the values of the 13 parameters of courtship were not systematically greater, or smaller, in the field compared with the laboratory ($F=0.435$; d.f.$=1,16$: $p=0.519$). However, when each parameter in the ANOVA is assessed individually, four of the thirteen were found to differ significantly: total courtship duration (118 ± 12 mins in lab cf. 232 ± 39 in field), number of pauses (63 ± 8 in lab cf. 119 ± 12 in field), number of bouts of Alternate Arm-Pulling (3 ± 1 in lab, cf. 10 ± 2) and number of sideways walks by the male (45 ± 10 in lab, cf. 13 ± 4). All of these differences are, to a greater or lesser extent, caused by the use of unnatural UV light to observe the courtships in the field. The scorpions can see UV, and as a result often cease their current behaviour when it is shone upon them. This results in more pauses, and therefore a greater courtship duration. In addition, the number of bouts of Alternate Arm-Pulling is significantly positively correlated with number of pauses, so interrupting the courtship increases their frequency. The difference in the number of sideways walks (a minor component of the courtship) may largely be due to the greater ease with which I could see and record the behaviours under the laboratory conditions. It therefore seems likely that the courtships observed in the laboratory colony were more "natural" than those observed in the field. The following description is therefore based on laboratory courtships.

The courtship behaviours can be classified into four categories: behaviours shown in early courtship (2%), behaviours shown throughout courtship (88%), behaviours shown in late courtship (9%) and behaviours associated with spermatophore deposition (1%). Unlike previously reported species of scorpion, *E. flavicaudis* begins its courtship within its crack, not upon the ground surface. Some 85% of the time spent in courtship occurred within cracks at Sheerness, although spermatophore deposition always occurred on the surface of the wall.

Courtships of these scorpions fall into two main categories. About 60% of courtships are preceded by a period of mate-guarding. This occurs when a vagrant male encounters a female either in the last stages of pregnancy, or whilst carrying young. As the female's receptivity is predictable, males will often stay with the female rather than search for one nearer receptivity (Benton, 1992b). The other 40% of courtships are not preceded by mate-guarding. These occur with females which were not pregnant and with females which were not found by males before becoming receptive after the period of maternal care.

The courtship of this species begins when a male takes hold of the female's pedipalpal claws in his own, with the male facing the female. During the time a male mate-guards he will turn from facing the entrance of the crack to facing the female at least once per night. He may then attempt to grab hold of her claws. During the time the female is carrying the young she will always repel him — but never violently (possibly because it may dislodge the young). On average 2 ± 0.5 days (range 1–6, $n = 12$) after the 1st instars moult, the female becomes receptive and does not repel the male's attempt to grab her.

Alternatively, if there has been no mate-guarding, the male will enter a novel crack very slowly, and upon encountering a female he will dart forwards very quickly and attempt to grab her claws. If this fails, the male will rapidly retreat (being "chased" by the female). Once on the surface the male pauses as the female retreats back down the burrow. He may then attempt to enter the crack again.

During the first half of the courtship the male usually stings the female several times (mean 3.6 ± 1.1 times, range 0–10, $n = 10$ courtships). The first sting can be anywhere on the female's body, but subsequent stings are invariably to one of the articulations of the female's pedipalps. In non mate-guarded matings the male will sting the female within seconds of grabbing her; if he manages to grab her on the first attempt the process is indistinguishable from a cannibalistic attack. During the time a male is stinging the female (which lasts on average 13.2 ± 3.0 min, range 0.5–52 min, $n = 22$) they are usually both still, though at first the female may try to retreat from the male. Occasionally the male may twist his sting in the wound. It was not possible to determine whether venom was injected into the wound, or whether it was purely a mechanical injury. In non mate-guarded courtships, females initially seem to struggle more and there is a tendency for the male to sting the female more often: 2.6 ± 0.8 ($n = 14$) stings in non mate-guarded courtships cf. 1.4 ± 0.5 ($n = 5$) stings in mate-guarded courtships (difference N.S.; data from fully, or partially, observed courtship in laboratory and field, when guarding status was also known).

The bulk of the courtship (in time and also the number of behaviours) is made from the following three component behaviours, which occur from the very start of the courtship until the final minutes:

(i) TUG: This is the most frequent behaviour shown during the courtship (mean 680 ± 122, range 290–1535 times per courtship, $n = 10$) (Fig. 1). The Tug consists of the male flexing his pedipalps and thereby drawing (or attempting to pull) the female towards him. The Tug is often accompanied by a backwards step by the male. Tugs occur throughout most of the courtship: they are missing from the last minutes, just before spermatophore deposition.

(ii) MALE-LED WALK: Unlike most other scorpions (see reviews by Garnier & Stockmann, 1972; Polis & Farley, 1979), the Promenade does not consist of long periods of the male leading the female passively around. In *E. flavicaudis* the male typically moves only a short distance (1–3 cm) at a time. The direction the male moves can be forwards (46 ± 7.0 times per courtship, $n = 10$), sideways (45 ± 9.7, $n = 10$) or backwards (95 ± 9.5, $n = 10$).

(iii) PAUSE: These were periods where the pair were immobile. These periods ranged from a few seconds to over an hour, but tended to be less than one minute on average (mean 53.8 ± 40.3 s, range 5–915 s, $n = 57$; data from 4 courtships, transcribed with accurate timing from audio tape).

Once the pair of scorpions have moved from their crack on to the wall surface other behaviours begin to occur, which signal the approach of spermatophore deposition. These include Shifting (where the male repeatedly walks forwards and backwards without ever moving far enough to cause the female to move); Arm-Pulling (the male repeatedly retracting and protracting his pedipalps thus causing the female's to do likewise) and Tail-Waving (the male sweeps the metasoma side-to-side over his body). Shifting occurs in 30.3 ± 6.6 ($n = 10$) bouts during a courtship, Arm-Pulling 40.0 ± 8.1, and Tail-Waving 20.1 ± 3.4. These behaviours are interspersed with Tugs, Male-Led Walks and Pauses.

One percent of the behaviours that occur within a courtship do so exclusively at its end, and are associated with spermatophore deposition. Immediately before deposition the male begins Alternate Arm-Pulling (which consists of regularly protracting and retracting the pedipalps, left and right alternately) and Vertical Tail-Waving (raising and

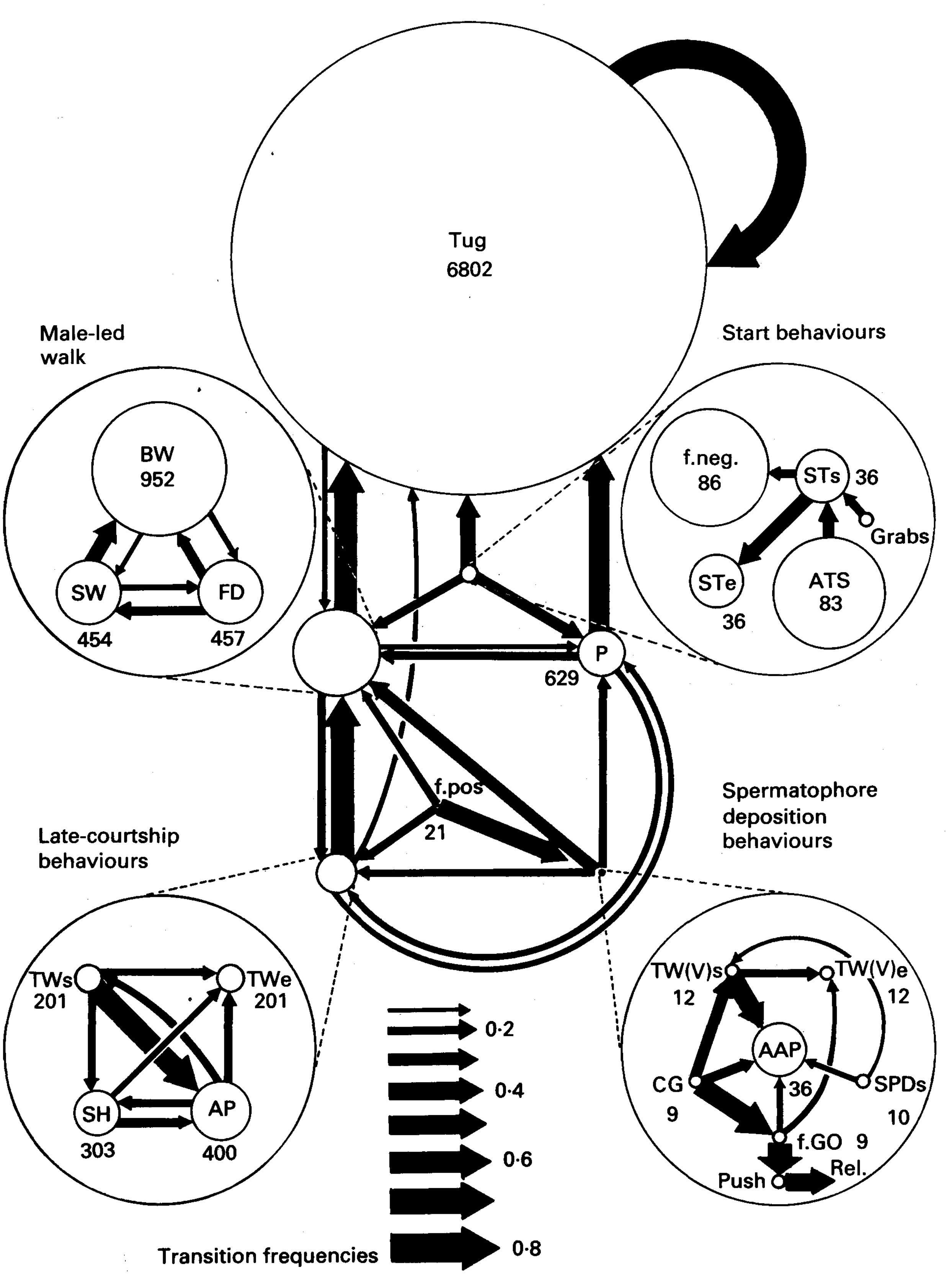

Fig. 1: Flow diagram of courtship behaviour of *Euscorpius*. Data from 10 courtships. Each circle represents a behaviour, and its size represents the total number of times that behaviour occurred in the 10 courtships. Arrows indicate transitions between behaviours (only transitions greater in frequency than 0.1 are shown). For clarity some behaviours are shown grouped. Abbreviations: grabs = male initiates courtship by taking hold of the female; STs = male begins to sting female; STe = male stops stinging female; ATS = male attempts to sting female; f.neg = "negative" female behaviours (e.g. trying to pull away from male); BW = male-led walk, backwards; FD = forwards walk by male; SW = sideways walk by male; P = pause; f.pos = female voluntarily advances towards male; TW = tail-waving (Tws = start, TWe = end); AP = arm-pulling; SH = shifting; TW(V) = tail-waving (vertically) (s = start, e = end); AAP = alternate arm-pulling; SPDs = spermatophore deposition starts; CG = cheliceral grip; fGO = female goes over spermatophore; Rel = male releases female. For descriptions of behaviours see text.

lowering the tail in the vertical plane). These behaviours are such good indicators of the imminent onset of deposition that it is possible they might be involved in the process. Perhaps both of these "pumping" behaviours help to expel the spermatophore from the paraxial glands by hydrostatic mechanisms.

Spermatophore deposition takes 2 min 26 s $\pm$ 4.6 s (n = 9). The base emerges first and is stuck to the substrate; the male then backs away from the spermatophore. The female approaches the male until their prosomas are in close proximity. The male, with his chelicerae, then takes a grip on the chelicerae of the female; this is in addition to the grip with his pedipalpal claws. At this time the female has moved over the spermatophore so that the sperm tube is located adjacent to her genital aperture. Over the next few seconds the male repeatedly raises and lowers his body, causing the female's to do likewise. Occasionally the male also "thrills" (Shulov & Amitai, 1958) the female's genital area, using his front pair of legs. These behaviours are likely to ensure exact positioning of the spermatophore. After a few seconds the male pushes sharply forwards, and this causes the female to move backwards with respect to the spermatophore, which flexes in the process causing sperm to be squeezed into her genital opening (see Fig. 2).

Once the sperm has been transferred the male first releases the female's pedipalps, then the chelicerae. The male then flees. After release, the female may retreat down her crack or may walk around the area with pedipalps spread wide. In this way she may find the spermatophore. In 75% (9/12) of occasions in the field the female searched for and found it. She then grips it with her chelicerae, pulls it from the wall and eats it. Old spermatophores (in both the field and laboratory) were often found on the wall surface, indicating that the female did not always search for and find the spermatophore.

Compared with other species, the courtship of *E. flavicaudis* is relatively simple (Benton, 1990). Unlike other scorpions' courtships (Benton, 1990, 1992c) during which there are different "phases", where different behaviours occur, the courtship of *Euscorpius* is relatively "homogeneous". The majority of the courtship (88% of the recorded behaviours) consists of Tugs, Male-Led Walks and Pauses — which occur from within minutes of the start to within minutes of the end (often in the sequence: Pause, *n* Tugs, Male-Led Walk, *n* Tugs, Male-Led Walk, *n* Tugs, Pause . . .). The length of the courtship seems to depend more on the time that it takes a male to "encourage" the female from her burrow (requiring Tugs and Male-Led Walks), than the time it takes to find a spermatophore deposition site. In the scorpion *Leiurus quinquestriatus* Hemprich & Ehrenberg the length of the courtship is proportional to the time that it takes for the male to encounter a suitable site on which to deposit the spermatophore (unpublished data). In *E. flavicaudis* the spermatophore is usually deposited very near to the crack entrance (field data: 5.7 $\pm$ 2.4 cm, range 1–29, n = 11) soon after the scorpions emerge from the crack, rather than after a long promenade covering many metres (as in *Paruroctonus mesaensis* Stahnke (Polis & Farley, 1979)).

Discussion

The majority of scorpion species studied are broadly similar in their courtship (Benton, 1990; Polis & Sissom, 1990). Typically, scorpion courtship begins with an introductory phase in which the male pacifies the female, usually with jerky movements of his body. This is followed by a promenade phase in which the male leads the female around until a suitable site on which to deposit the spermatophore is found. Following the promenade phase new behaviours appear and later spermatophore deposition occurs.

Euscorpius flavicaudis has a quite different courtship. It is relatively homogeneous, without an obvious introductory phase, promenade phase, or spermatophore deposition phase. The only "introductory" behaviour shown is the "sexual stinging" (Francke, 1979). The majority of the courtship consists of three main behaviours: the Tug, Male-Led Walk and Pause. Behaviours associated with spermatophore deposition appear gradually in the last half-hour or so of the courtship. It is unusual in that much

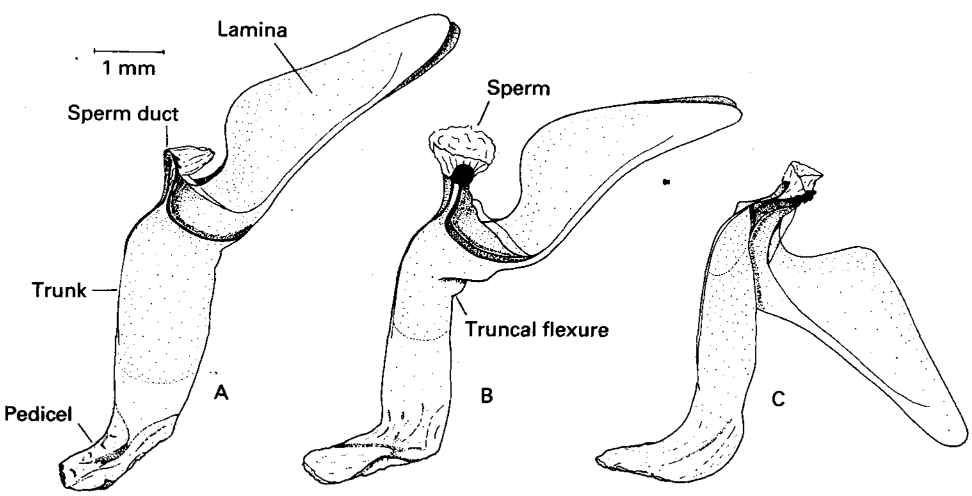

Fig. 2: The lamelliform spermatophore of *Euscorpius*. Views are all lateral, drawn to same scale. Male faces towards the left in the diagram. **A** Pre-insemination spermatophore; **B** After deposition, the female goes over the spermatophore, so that her genital opercula engage in the gap between lamina and trunk. Backwards movement by the female causes the spermatophore to pivot at the base, thus depressing the lamina causing the spermatophore to kink at the truncal flexure and squeeze the sperm out. **C** Post-insemination spermatophore.

of the courtship occurs within the burrow of the female (though this may just be a reflection of the way most data on scorpion courtship have been gathered). Possible reasons for these differences are:

1. The function of the introductory phase in the courtship of other scorpions is probably to reduce cannibalism (Polis & Farley, 1979; Benton, 1992c). In *E. flavicaudis* at Sheerness, many of the courtships occur between males and females that have been cohabiting. In these cases, females will already have had the possibility of identifying their cohabitant, making the Introductory Phase of other species' courtship redundant. *Euscorpius* is also relatively unusual in that the adult males can be larger than adult females. In most scorpion species the male is usually lighter and more slender than the female (Cloudsley-Thompson, 1968; pers. obs.). Indeed, the main offensive weapons of *E. flavicaudis* are their claws, and those of the male are usually larger, often considerably so (Benton, 1991b). This means that it is often the female that is at risk of sexual cannibalism, so she may capitulate to a male without the aggression that characterises other species' courtship.

2. All other reports of scorpion courtships are of the courtship being initiated on the surface of the ground. In *E. flavicaudis* at Sheerness, by far the majority of courtships were initiated within the female's crack. Owing to the predictability of the mating season, females can predict that males will become vagrant, and that any scorpion entering the crack is likely to be a mature male. This is different from other species meeting on the surface, where, if a male grabs a female she must respond as if he were a predator, because without visual or chemical communication she cannot a priori identify him as a mate.

3. The duration of courtship is largely determined by the time it takes the male to pull the female from the crack. In other species one of the major determinants of courtship length is the time taken to find a suitable spermatophore deposition site (Polis & Sissom, 1990; Benton, 1990). Owing to the extreme uniformity of their habitat at Sheerness, this takes little time. They have no need of a promenade phase in their courtship.

Females will, in general, only mate once each year. They will also mate with any male present at the right time, irrespective of his size or whether he has mate-guarded her. There is a low rate of courtships being aborted once they have begun (less than 15% observed failure rate, possibly an inflated figure owing to my presence). Once courtship has begun, sperm-transfer usually follows (this can be determined from the shape of the spermatophore, see Fig. 2). There are no obvious differences in the courtship between cohabiting scorpions and between scorpions for whom this is the first encounter, other than in the first few minutes (in non mate-guarded courtships the female is much more likely to struggle and also more likely to be stung more times). It therefore seems unlikely that females are using the courtship to assess the "quality" of males. Instead, the length and complexity of the courtship can perhaps be explained by three factors. First, the early stages of the courtship reduce cannibalism between disparate-sized partners (especially large females and small males, when there has been no cohabitation). Secondly, as the scorpions do not leave the shelter of the female's crack until the female is ready and willing to mate, the time spent out of the crack is minimised and the chance of predation is reduced. Thirdly, the final stages of the courtship serve to locate a suitable site for deposition of the spermatophore, and transfer of sperm.

References

ALEXANDER, A. J. 1956: Mating in scorpions. *Nature, Lond.* **178**: 867–868.

ANGERMANN, H. 1955: Indirekte Spermatophorenübertragung bei *Euscorpius italicus* Hbst. (Scorpiones, Chactidae). *Naturwissenschaften* **42**: 323.

AUBER-THOMAY, M. 1974: Croissance et reproduction d'*Androctonus australis* (L.) (Scorpions, Buthides). *Annls Sci.nat.* (Zool.) (12)**16**: 45–54.

BAERG, W. J. 1954: Regarding the biology of the common Jamaican scorpion. *Ann.ent.Soc.Am.* **47**: 272–276.

BENTON, T. G. 1990: *The behaviour and ecology of scorpions.* Unpublished PhD thesis, University of Cambridge.

BENTON, T. G. 1991a: Reproduction and parental care in the scorpion *Euscorpius flavicaudis*. *Behaviour* **117**: 20–27.

BENTON, T. G. 1991b: The life history of *Euscorpius flavicaudis* (Scorpiones, Chactidae). *J. Arachnol.* **19**: 105–110.

BENTON, T. G. 1992a: The ecology of the scorpion *Euscorpius flavicaudis* in England. *J.Zool.,Lond.* **226**: 351–368.

BENTON, T. G. 1992b: Determinants of male mating success in a scorpion. *Anim.Behav.* **43**: 125–135.

BENTON, T. G. 1992c: Courtship and mating in *Leiurus quinquestriatus* (Scorpiones: Buthidae). *In* J. E. Cooper, P. Pearce-Kelly & D. L. Williams (eds.), *Arachnida*: 83–98. Chiron Publications.

BRONGNIART, C. & GAUBERT, P. 1891: Fonctions de l'organe pectiniforme des Scorpions. *C.r.hebd.Séanc.Acad.Sci.,Paris* **113**: 1062.

BUCHERL, W. 1956: Escorpiões e escorpionismo no Brasil. *Mems Inst. Butantan* **27**: 121–155.

CLOUDSLEY-THOMPSON, J. L. 1968: *Spiders, scorpions, centipedes and mites* (2nd edn). 1–278. Pergamon Press.

CLOUDSLEY-THOMPSON, J. L. 1990: Scorpions in mythology, folklore and history. *In* G. A. Polis (ed.), *The biology of scorpions*: 462–485. Stanford Univ. Press, Stanford, Calif.

FABRE, J. H. 1923: *The life of the scorpion* (Transl. A. T. de Mattos). 1–344. Hodder & Stoughton, London.

FRANCKE, O. F. 1979: Observations on the reproductive biology and life-history of *Megacormus gertschi* Diaz (Scorpiones: Chactidae: Megacorminae). *J.Arachnol.* **7**: 223–230.

GARNIER, G. & STOCKMANN, R. 1972: Étude comparative de la pariade chez différentes espèces de scorpions et chez *Pandinus imperator*. *Annls Univ.Abidjan* (E)**5**: 475–497.

MACHAN, L. 1968: Spectral sensitivity of scorpion eyes and the possible role of shielding pigment effect. *J.exp.Biol.* **49**: 95–105.

POLIS, G. A. & FARLEY, R. D. 1979: Behavior and ecology of mating in the cannibalistic scorpion, *Paruroctonus mesaensis* Stahnke (Scorpionida: Vaejovidae). *J.Arachnol.* **7**: 33–46.

POLIS, G. A. & SISSOM, W. D. 1990: Life history. *In* G. A. Polis (ed.), *The biology of scorpions*: 161–223. Stanford University Press, Stanford, Calif.

SHULOV, A. & AMITAI, P. 1958: On the mating habits of three scorpions: *Leiurus quinquestriatus* H. et E., *Buthotus judaicus* E. Sim. and *Nebo hierichonticus* (E. Sim.). *Archs Inst.Pasteur Alger* **36**: 351–369.

VACHON, M. 1953: The biology of scorpions. *Endeavour* **12**: 80–89.

ZOLESSI, L. C. de 1956: Observaciones sobre el comportamiento sexual de *Bothriurus bonariensis* (Koch) (Scorpiones, Bothriuridae). *Boln Fac.Agron.Montevideo* **35**: 1–10.