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EFFECTS OF SIZE, MOTILITY AND PARALYSATION TIME OF PREY ON THE QUANTITY OF VENOM INJECTED BY THE HUNTING SPIDER *CUPIENNIUS SALEI*

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Summary

Previous experimental studies have shown that neotropical wandering spiders (*Cupiennius salei*) inject more venom when attacking larger crickets. It has been postulated that this is a consequence of predator–prey interactions during envenomation, which increase in intensity with the size of a given prey species. The present study was designed to test this hypothesis using anaesthetized crickets of different sizes that were moved artificially. *Cupiennius salei* was found (1) to inject more venom the greater the intensity of the struggling movement of the crickets (prey size kept constant); (2) to inject more venom the longer the duration of the struggling movement of the crickets (prey size and intensity of movement kept constant); and (3) to inject equal amounts into crickets of different size (duration and intensity of movement kept constant).

These results indicate that *C. salei* alters the amount of venom it releases according to the size and motility of its prey. Venom expenditure depends mainly on the extent of the interactions with the prey during the envenomation process, whereas prey size is of minor significance. The regulation of venom injection in concert with behavioural adaptations in response to various types of prey minimizes the energetic cost of venom production, thus increasing the profitability of a given prey item.

Key words: spider, *Cupiennius salei*, synthetic stimulation, venom injection, venom quantity, prey capture.

Introduction

The use of venom is of great importance for the feeding success of most spiders. It is particularly important for non-web-building spiders because they have few morphological features to help them subdue their prey. They possess comparatively fast-acting venoms of high potency that reduce the risk of long and dangerous struggles (Bettini and Brignoli, 1978). Smaller prey are caught by these spiders than by social spiders or web-building species because they lack silk as a capturing tool (Enders, 1975; Nentwig and Wissel, 1986; Rypstra and Tirey, 1991). This could also be a result of limited venom reserves, since the quantity of venom that can be obtained from spiders is quite small (Bücherl, 1971; Perret, 1974; Malli et al., 1993). After complete depletion of the paired venom glands, it takes from a few days to several weeks for the venom to regenerate (Perret, 1977; Boevé et al., 1995).

Recent evidence has shown that the neotropical wandering spider *Cupiennius salei* reduces the energetic costs of venom production by controlling the quantity expended when feeding on crickets of different size (Malli et al., 1998). Prey size is considered to be an important determinant of the acceptability of a given prey item (Bristowe, 1958; Enders, 1975; Riechert and Luczak, 1982; Forster, 1985; Nentwig and Wissel, 1986; Rypstra, 1990). Once the prey item has been accepted, however, it is more likely that the venom dose is regulated by interactions with the prey. Boevé et al. (1995) suggested that *Cupiennius salei* injects more venom into prey that is ‘difficult to handle’ than into prey that is ‘easy to handle’, but they did not determine the amount of venom injected.

Insects, which are the main prey group of spiders, vary in size, palatability, susceptibility to venom (Friedel and Nentwig, 1989; Kuhn-Nentwig et al., 1998) and mechanical defence. Therefore, from an energetic point of view, it would be wasteful for a spider to inject more venom than required into a large but comparatively susceptible prey. In the field, these factors cannot readily be separated from each other by investigators, making it difficult to determine the extent to which they influence the quantity of venom expended. In crickets, for example, larger individuals produce stronger leg kicks and are also less susceptible than smaller individuals to venom. To establish the influence of these two factors on prey capture, anaesthetized crickets were moved artificially and offered to wandering spiders (*Cupiennius salei*) to elicit envenomation behaviour. By this means, it was possible to vary independently the size, intensity of movement and paralysation time of the prey in order to determine the effects on the quantity of venom expended. The mass of the venom released was determined by enzyme-linked immunosorbent assay (ELISA).

In this study, we present the result of experiments designed to test the following three hypotheses: (1) *C. salei* injects more venom into crickets of the same size the greater the intensity of their struggling movements; (2) *C. salei* injects less venom the faster that crickets of the same size and with the same intensity of struggling movement are paralysed; and (3) *C. salei* injects equal amounts of venom into crickets of different sizes when the intensity of their movement is equal.

Materials and methods

Spiders

Three breeding stocks of mature female wandering spiders *Cupiennius salei* Keyserling were used for the experiments. The stocks were obtained from a permanent breeding line that has been maintained for several years. The spiders were housed separately in 2 l glass jars at a room temperature of 20–25 °C and with a light:dark regime of 12 h:12 h (Malli et al., 1993). They were fed weekly with *Gryllus* sp. to avoid habituation to the test prey, *Acheta domesticus.*

Apparatus

To test the influence of the struggling movements of the prey, the speed of paralysis and prey size on the quantity of venom expended, the procedure illustrated in Fig. 1 was employed. The prey (*Acheta domesticus*) was tethered, using a transparent plastic thread (diameter 0.1 mm; length 80 cm) placed immediately behind the pronotum between the first and second pair of legs, to a wooden ball (diameter 12 mm; mass 1.2 g) laid on a rotating rubber conveyor belt. Nine cross-strips of rubber (height 1.0–2.5 mm) were attached to the belt at irregular intervals. The speed of the conveyor belt could be varied between 0 and 120 rotations min^{-1}. As the conveyor belt rotated, the wooden ball was carried forward a fraction until it jumped backwards over the cross-strips as a result of the resistance caused by the spider holding the prey back with its chelicerae. In this way, irregular movements of pre-anaesthetized prey items could be simulated artificially.

To visualize the artificial stimuli, the thread was attached to the membrane of an 8 Ω loudspeaker subsequent to the spider experiments. The membrane vibrations were then recorded as acoustic signals and visualized by a 16-bit audio sound card (creative wave studio; Creative Technology Ltd), as shown in Fig. 2. The physical parameters of the stimuli were not analysed in detail. The amplitude therefore represents the relative intensity of simulated prey activity recorded during a 10 s period (the control shows the background noise of the apparatus). In experiments, stimuli with a low (15 rotations min^{-1}), a medium (33 rotations min^{-1}) or a high (67 rotations min^{-1}) intensity were applied as the experimental treatment variable.

Experimental design

Each hypothesis was tested in a separate experiment. In all experiments, a standard procedure was adopted: 20 spiders from one breeding stock were divided into four groups of five individuals. Each individual in a group underwent four treatments. Each treatment was applied twice with a 14 day interval between treatments. The treatments were randomly selected such that, by the end of the experiment, all five spiders in a group had been exposed twice to each of the four treatments. In each test, a single cricket was anaesthetized with

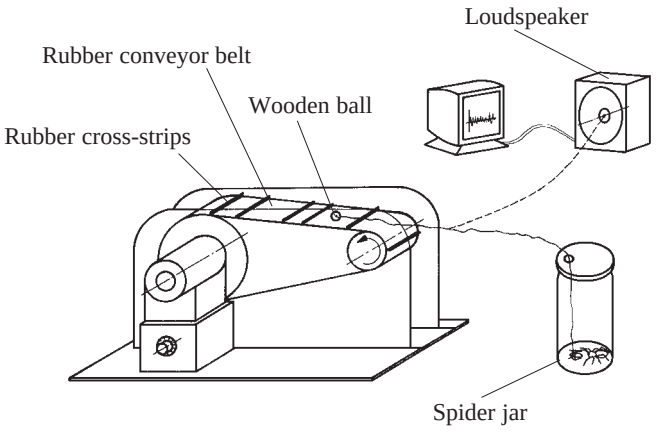

Fig. 1. Experimental apparatus. Pre-anaesthetized crickets were tethered, using a plastic thread, to a wooden ball placed on a rubber conveyor belt to which rubber cross-strips were attached at irregular intervals. Artificial movements of the crickets could be simulated by rotation of the belt. The movements were visualized subsequent to the spider experiments by attaching the thread to the membrane of a loudspeaker. The membrane vibrations were then recorded as acoustic signals and visualized using a 16-bit audio sound card.

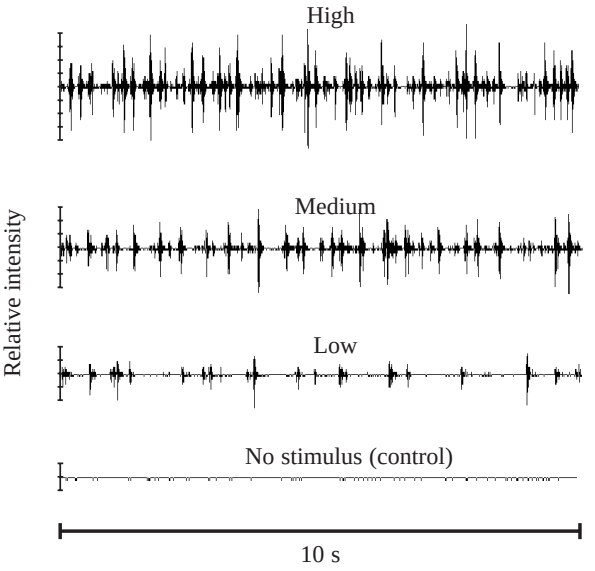

Fig. 2. Example of the output from the 16-bit audio sound card. Artificial stimuli were visualized by attaching the plastic thread, normally used to tether the prey, to the membrane of an 8 Ω loudspeaker. The acoustic signals were then recorded by a 16-bit audio sound card. Stimuli of high, medium or low intensity were applied during the experiments. The control represents the background noise of the apparatus.

CO_2, weighed and tied up with thread. Previous tests showed that the CO_2 anaesthesia lasts for at least 12 min so that the crickets would not recover during the experiment. The cricket was then lowered through a small hole (diameter 18 mm) into a glass jar, where it was offered to a spider. As soon as the cricket had been bitten, the rotation of the apparatus was started, at an intensity and for a duration appropriate to the treatment being tested. Exactly 5 min after the initial bite, the cricket was removed from the spider using a soft paint brush, weighed and homogenized 2 min later in 3 ml of 0.2 mol l^{-1} carbonate/bicarbonate buffer, pH 9.5. The homogenates were placed in an ice-cooled ultrasonic bath (Tec-25, Telsonic, Switzerland) for 1 h and were subsequently centrifuged for 1 min at 10 000 ***g*** at 4 °C. The supernatants were divided into samples of 350 µl and stored at −30 °C until required. The treatments varied between experiments as follows.

Influence of the intensity of prey movement (hypothesis 1)

The influence of the speed of paralysis (duration of the experiment) and prey size was kept constant while the intensity of prey movement was varied artificially. At 14 day intervals, each of the 20 spiders was randomly selected and offered a single cricket of 290–320 mg body mass, artificially moved for 5 min using a high-, medium- or low-intensity stimulus (Fig. 2). In the control experiment, the crickets were left in the chelicerae of the spider for 5 min without any additional stimulus.

Influence of paralysation time (hypothesis 2)

The intensity of prey movement was kept constant, and only the duration of the stimulus was varied, thus simulating the time taken to reach paralysis. At 14 day intervals, each of the 20 spiders from the second breeding stock was randomly selected and offered a single cricket of the same mass (290–320 mg), stimulated at the same intensity (medium, Fig. 2) for four different durations. In the three experimental treatments, the artificial stimulus continued for 1, 2.5 or 5 min after the initial bite, whereas in the control experiment, no stimulus was applied.

Influence of prey size (hypothesis 3)

The effect of prey size on the quantity of venom expended was tested by keeping both the duration and the intensity of a given stimulus constant. For this purpose, 20 spiders from the third breeding stock were randomly selected and fed at 14 day intervals with a single cricket in each of the following size classes: 100–110 mg, 290–320 mg, 420–460 mg and 600–660 mg. All prey items were artificially moved at the same intensity (medium, Fig. 2) and for the same duration (5 min). In this experiment, the two larger size classes were homogenized with 5 ml of carbonate/bicarbonate buffer.

Determination of the quantity of venom injected

The quantity of venom expended on each prey item was measured by enzyme-linked immunosorbent assay (ELISA) of whole-cricket homogenates (for more details, see Malli et al., 1998). In brief, thawed whole-cricket homogenates were used to coat 96-well microtitre plates in triplicate. After blocking the remaining protein binding sites with 1 % bovine serum albumin, the monoclonal antibody 9H3 was added. This antibody recognizes *Cupiennius salei* toxin 1 (CSTX-1), the main toxin of *C. salei* venom, and cross-reacts with a second toxin, *Cupiennius salei* toxin 2 (CSTX-2). After several washes in 0.9 % NaCl, 0.1 % Tween 20, a goat anti-mouse IgG peroxidase-conjugated antibody was added. After several further washes, the reaction was visualised by incubating with the enzyme substrate, after which the absorption of each well was read at 405 nm/490 nm using a multiscan ELISA plate reader (MR500, Dynatech). Each microtitre plate contained standards consisting of homogenates of crickets of matching size artificially injected with different amounts of venom and subsequently prepared in the same manner as the experimental crickets. Standard curve-fitting techniques and calculations of the venom quantity were made using BioLinx 2.20 software (Dynatech).

Results

Prey-capture behaviour of spiders

The experimental spiders exhibited a normal pattern of prey-capture behaviour (Melchers, 1963, 1967) when presented with pre-anaesthetized crickets during the experiments. The spiders waited in a motionless state and immediately bit the secured cricket when it reached the bottom of the glass jar. The plastic thread had no observable influence on envenomation behaviour. At the highest stimulus intensity, the spiders held the prey in their chelicerae and showed no signs of retreat. In the experiments, most crickets were bitten in the thoracic region (87.4 %), with 12 % of bites in the soft abdomen and 0.6 % in the head capsule.

Crickets lost between 5.75 and 12.33 mg of their body mass during the 5 min exposure to the spiders. The loss of body mass was not significantly different between the treatments in any of the hypotheses tested (P>0.05, Friedman test), which indicates a constant sucking rate, irrespective of prey size or of the duration and intensity of the stimulus.

C. salei has been observed on occasion to start wrapping its prey with silk prior to eating it (Malli et al., 1998). In the experiments testing hypothesis 2 (the influence of paralysation time), the time taken to wrap the prey after the initial attack was recorded. The number of prey items wrapped with silk declined with increasing levels of prey movement, so that while 80 % of control items (no movement) were wrapped, 67.5 % were wrapped when the prey was artificially moved for 1 min, 42.5 % were wrapped after 2.5 min of movement and only 7.5 % after 5 min of movement.

Quantity of venom expended

Influence of the intensity of prey movement (hypothesis 1)

The quantity of venom injected into crickets of the same mass (290–320 mg), artificially moved at four different intensities, is shown in Fig. 3A. Twenty values were obtained for each treatment, consisting of the average of two trials in

Table 1. *Probability values for comparisons among treatments for each experimental hypothesis (nonparametric Quade test)*

Type of stimulus	No stimulus	Low	Medium	High
Hypothesis 1: influence of the prey response				
No stimulus	–	$P>0.25$*	$P<0.025$	$P<0.001$
Low		–	$P<0.050$	$P<0.001$
Medium			–	$P<0.005$
High				–
Type of stimulus	**No stimulus**	**1 min**	**2.5 min**	**5 min**
Hypothesis 2: influence of paralysation time				
No stimulus	–	$P>0.05$*	$P<0.001$	$P<0.001$
1 min		–	$P<0.050$	$P<0.001$
2.5 min			–	$P<0.001$
5 min				–
Type of stimulus	**100–110 mg**	**290–320 mg**	**420–460 mg**	**600–660 mg**
Hypothesis 3: influence of prey size				
100–110 mg	–	$P<0.005$	$P<0.005$	$P<0.001$
290–320 mg		–	$P>0.40$*	$P>0.25$*
420–460 mg			–	$P>0.25$*
600–660 mg				–

*Null hypothesis (equal venom quantities) is not rejected.

which each spider was tested twice per treatment. The mean values ranged from 0.73±0.33 µl (mean ± S.D.) for control items (not moved), to 1.61±0.81 µl for crickets moved at high stimulus intensity. The mean values for low- and medium-intensity stimulation of prey items were 0.77±0.42 µl and 1.13±0.49 µl respectively. The fifth/ninety-fifth percentiles show that the amount of venom expended varied within a treatment, particularly when the stimulus intensity was high. The largest amount that was injected by a single spider was 4.99 µl, measured in a highly stimulated cricket, representing nearly half the amount that could be milked from adult females (Malli et al., 1993).

The nonparametric Quade test for related samples (Conover, 1980) showed a highly significant relationship between the intensity of stimulation and the quantity of venom expended ($P<0.001$). Multiple comparisons indicated that *C. salei* released significantly more venom as the intensity of prey movement increased (Table 1, hypothesis 1). Volumes of venom injected into control crickets (not stimulated) and weakly stimulated crickets did not differ significantly from each other ($P>0.25$).

Influence of paralysation time (hypothesis 2)

The effect of the simulated prey movement on the quantity of venom injected is shown in Fig. 3B. Box plots are derived from 20 values obtained from each of four different treatments. Each value is the average of two trials performed on each spider. The duration of the stimulus and the quantity of venom expended were positively correlated ($r=0.61$, $P<0.01$; Pearson correlation). The quantity of venom injected increased from 0.53±0.33 µl in control crickets to 0.75±0.36 µl in crickets artificially moved for 1 min, 0.9±0.44 µl in crickets artificially moved for 2.5 min and 1.19±0.34 µl in crickets artificially moved for 5 min.

The relationship between the duration of prey movement and the quantity of venom expended was highly significant ($P<0.001$; Quade test). Multiple comparisons between the four treatments are shown in Table 1 (hypothesis 2). Crickets stimulated for 1 min did not receive significantly more venom than control prey items ($P>0.05$). In all other comparisons, *C. salei* released significantly less ($P<0.05$) venom the shorter the prey movement, i.e. the faster the prey was paralysed.

Influence of prey size (hypothesis 3)

The quantity of venom injected into four size classes of artificially moved prey is shown in Fig. 3C. Box plots are derived from 20 values for each size class which represent the average of two trials on each spider. The mean values ranged from 0.44±0.45 µl for the smallest (class I; 100–110 mg) to 0.91±0.64 µl for the largest (class IV; 600–660 mg) size class (0.84±0.60 µl for size class II and 0.86±0.70 µl for size class III, respectively). The fifth/ninety-fifth percentiles show that the quantity of venom released varied widely within a size class. Prey size and the quantity of venom expended were weakly correlated ($r=0.23$, $P<0.05$, Pearson correlation). The nonparametric Quade test for related samples showed that at least one size class was different from all others ($P<0.01$). Multiple comparisons among size classes are shown in Table 1 (hypothesis 3). *C. salei* injected significantly less venom into the smallest size class ($P<0.005$), whereas the null hypothesis (equal amounts) cannot be rejected for comparisons between the other three size classes ($P>0.05$).

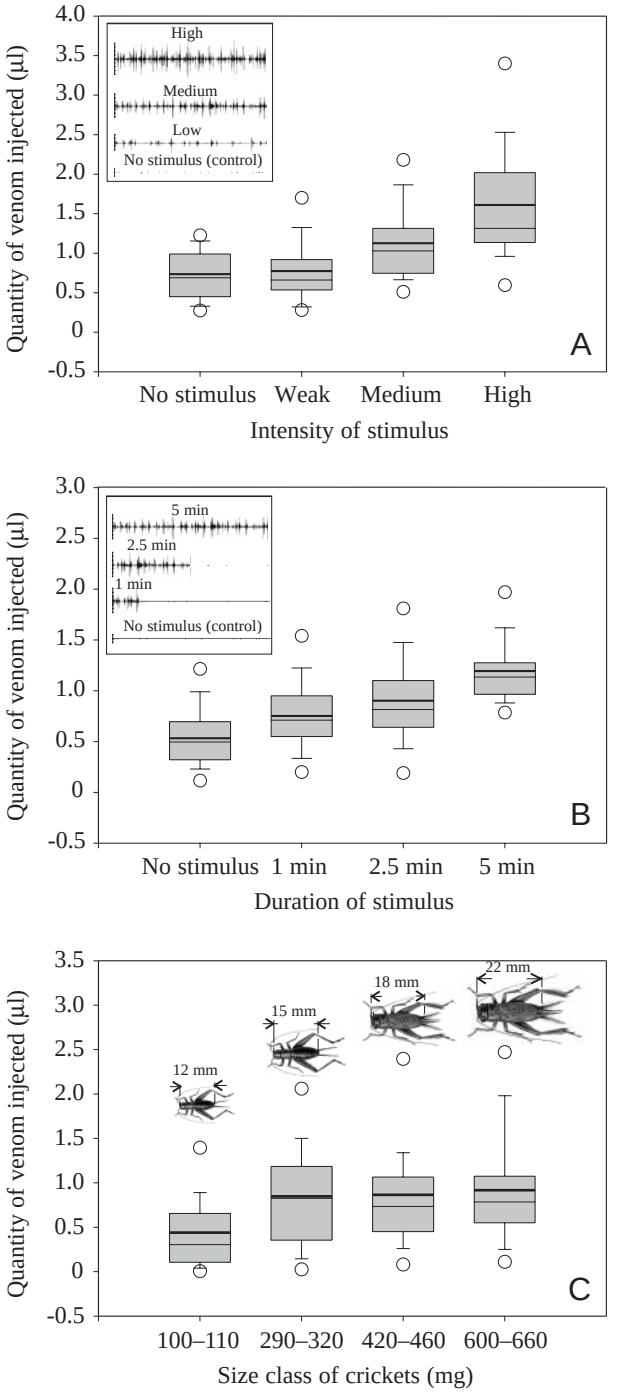

Fig. 3. Quantity of venom injected by *Cupiennius salei* into artificially moved crickets. Twenty spiders were used in each of three independent experiments. Each spider was fed randomly at 14 day intervals on a single pre-anaesthetized cricket treated according to the hypothesis being tested (see below). 5 min after the initial bite, the cricket was removed from the spider and homogenized 2 min later. Each spider was tested twice in each treatment. The quantity of venom expended was measured by enzyme-linked immunosorbent assay (ELISA) of whole-cricket homogenates. Box plots show the median and the twenty-fifth/seventy-fifth percentiles. Error bars represent the tenth/ninetieth percentiles, open circles the fifth/ninety-fifth percentiles and thick solid lines the mean values. (A) Influence of the intensity of prey movement (hypothesis 1). Each spider was fed a single cricket (290–320 mg) which was artificially moved for 5 min at high, medium or low intensity (no movement for the control). The inset shows the relative intensities and frequency contents of the stimuli. The control is the background noise of the test apparatus. (B) Influence of paralysation time (duration of stimulus) (hypothesis 2). Each spider was fed a single cricket (290–320 mg) that was moved for 5, 2.5, 1 or 0 min (=control) at medium intensity. The inset shows the relative intensities, frequency contents and durations of the stimuli. The control is the background noise of the test apparatus. (C) Influence of prey size (hypothesis 3). Each spider was fed a single cricket, moved for 5 min at medium intensity, in one of the following size classes: 100–110 mg, 290–320 mg, 420–460 mg or 600–660 mg.

Comparisons among the hypotheses

Comparisons were made between the experiments since some of the treatments were carried out in exactly the same way. Spiders from the first breeding stock, tested in hypothesis 1, did not differ significantly in the amount of venom injected into control prey from spiders tested in hypothesis 2 ($P>0.05$, Mann–Whitney *U*-test). There was no significant difference between crickets stimulated with a medium-intensity stimulus for 5 min (hypothesis 1) and crickets stimulated for 5 min at medium intensity in hypothesis 2 ($P>0.25$, Mann–Whitney *U*-test). The quantity of venom injected into size class II crickets (290–320 mg) following 5 min of artificially simulated medium-intensity movement were compared between all three experiments. There were no significant differences in the quantities of venom injected among the three groups of spiders ($P>0.05$, Kruskal–Wallis test).

Discussion

There is experimental evidence that spiders are able to regulate the quantity of venom expended according to prey size (Perret, 1977; Pollard, 1990; Boevé et al., 1995; Malli et al., 1998). Larger prey items do not necessarily require more venom to be immobilized than smaller ones. This is because the susceptibility to the venom of a given spider can vary from one prey species to another, independently of size (Friedel and Nentwig, 1989; Kuhn-Nentwig et al., 1998). It was therefore hypothesized that reliable regulation of venom expenditure by the spider can only be achieved by the determination of the degree of paralysis of the target prey. This study presents the results of experimental testing of this hypothesis.

Prey-capture behaviour

The prey-capture behaviour of experimental spiders when offered anaesthetized crickets was similar to that described for living prey (Melchers, 1967). This was probably due to small movements or vibrations occurring as the prey was placed into the glass jar. Airborne and substratum-borne vibrations are reported to be significant factors in stimulating predatory behaviour in *C. salei* (Barth, 1982). Their vision is poorly

developed (Melchers, 1967; Barth, 1982) and is not, therefore, a suitable tool for discriminating prey size.

Other elements of the prey-capture behaviour were similar to those of a recent study (Malli et al., 1998). The majority of crickets were bitten in the sensitive thoracic region, which may decrease the time necessary to complete immobilization and, therefore, reduce the risk of injury. The loss of body mass by the crickets during the 5 min exposure to the spiders indicates that *C. salei* simultaneously injects venom and sucks out the body fluids of the prey. Since leaking haemolymph dries up within a few minutes, it makes sense for the spider to suck up the body fluids immediately. Post-immobilization wrapping of larger prey was shown to be time-dependent, which suggests that the absence of vigorous movements by the prey is a necessary element of the stimulus initiating wrapping. Post-immobilization wrapping by *C. salei* is similar to that of the closely related lycosid spiders (Rovner and Knost, 1974; Greenquist and Rovner, 1976), which has been postulated to be a behavioural adaptation for life in the herbaceous stratum, reducing the possibility of losing the prey when it is released from the cheliceral grasp. In the field, *C. salei* lives and hunts for prey on banana plants, agaves and aloes (Barth and Seyfarth, 1979), where this behaviour would also aid hunting success.

Quantity of venom injected

Influence of the intensity of prey movement

The experimental results showed that *C. salei* injects more venom when prey size is kept constant and the intensity of movement increases (Fig. 3A). Injection of larger quantities of venom into vigorously resisting prey serves for quick immobilization, thus preventing the spider from severe injuries or from losing its prey. Although no quantitative data are available, it can be assumed that venom production is energetically costly: in *C. salei*, it takes over a week for depleted venom reserves to regenerate fully (Boevé et al., 1995). The regulation of venom injection is, therefore, an excellent way of reducing the metabolic costs of venom production. Spiders saved up to 50 % of their venom by discriminating between high-intensity prey movements and low-intensity movements. Moreover, an unnecessary depletion of its venom reserves would leave the spider defenceless and unable to hunt prey for a certain period.

Weakly stimulated crickets did not receive significantly more venom than control items, presumably because the stimulus produced by them was below the range of discrimination and, therefore, no additional venom was released by the spider.

Influence of paralysation time

The second experiment provided evidence that *C. salei* regulates its venom release gradually in response to the degree of paralysis of the target prey (Fig. 3B). Only crickets that were moved for 1 min did not differ significantly from control items (no stimulation) in the amount of venom injected. This stimulus duration was probably too short to reveal a difference between the quantity that was initially injected and any additional venom release.

Influence of prey size

The experimental results confirmed the third hypothesis, that *C. salei* injects equal amounts of venom into prey of different size when the intensity and duration of their movements were equal (Fig. 3C). This indicates that prey size alone is not likely to be an important cue for effectively regulating venom injection. This clearly explains the results of Malli et al. (1998), who performed exactly the same experiment with live as opposed to artificially moved crickets. They showed that *C. salei* released significantly more venom when attacking larger prey. Our results suggest that this was a consequence of predator–prey interactions during envenomation, which increase with the size of a given prey species, but did not depend on the size of the prey itself. When a prey item falls below a certain size range, it will be subdued by mechanical means rather than by venom injection. This assumption is supported by the results of Malli et al. (1998), who showed that no venom was detectable in 22 % of the smallest crickets. In our experiment, in which crickets were moved artificially, each of the smallest crickets received a certain amount of venom, but this was significantly less than the amount injected into the three larger size classes.

Size is considered to be an important determinant of the acceptability of a given prey item (Bristowe, 1958; Enders, 1975; Riechert and Luczak, 1982; Forster, 1985; Nentwig and Wissel, 1986; Rypstra, 1990). However, despite matching the acceptable size range of a polyphagous spider, a prey can vary in its taste, vulnerability, mechanical defence and susceptibility to the venom of the spider (Riechert and Luczak, 1982; Kuhn-Nentwig et al., 1998). This evidence, together with the results of our experiments, suggests that size alone is not a reliable parameter for the effective regulation of venom injection by the spider because of the variability of other aspects of prey susceptibility.

In conclusion, it has been shown that *C. salei* injects venom gradually in response to stimuli generated during interactions with the prey in the course of the envenomation process. This regulation, together with behavioural adaptations, serves to minimize the energetic cost of venom production and therefore increases the profitability of the prey. It is not clear how the stimuli produced by the prey are sensed nor to what extent they can be discriminated by the spider. It is known that *C. salei* is able to identify and discriminate vibrations transmitted through the air or the substratum (Barth, 1982, 1985, 1993; Hergenröder and Barth, 1983a,b). During envenomation, however, the so-called ‘contact vibrations’ are probably more important. Contact vibrations have rarely been studied in detail, mainly because they are difficult to record and to quantify. There is ample evidence, however, that they are a common and important means of communication during the contact phases of sexual, aggressive or parent–offspring interactions as well as during predator–prey encounters (Markl, 1983). Detailed observations of the capture behaviour of *C.*

salei have revealed that the first and second pairs of legs were only used within the first few seconds of an attack (Melchers, 1967). The legs were withdrawn as soon as possible, and the prey was held with the chelicerae alone until it was completely paralysed. Even the palps were not in close contact with prey during capture. Sense organs for the detection of the stimuli emitted by the prey should, therefore, be located either directly on the chelicerae or close to them. Among the candidate receptors are tactile hairs and the slit sense organs that are only found on the appendages, including the chelicerae (Barth and Libera, 1970; Peters and Pfreundt, 1983). In *C. salei*, tactile hairs and the slit sense organs are found all over the chelicerae and are concentrated at the base of the claws (Barth and Libera, 1970; F. G. Barth and O. Friedrich, personal communication). Slit sense organs are reported to be the most sensitive receptors for vibrations transmitted through solid substrata (Barth, 1985). Whether they may serve additional vibrosensitive functions, for example, controlling the release of venom during envenomation, remains to be demonstrated experimentally.

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