Contact Chemoreception of Prey in Hunting Scorpions (Arachnida: Scorpiones)

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Abstract

Scorpions commonly are assumed to hunt on living prey. But under laboratory conditions they also respond very sensitively to dead insects lying on the substrate. In many cases the motionless prey is seized and consumed. It was investigated how this behavior can be elicited.

The buthid scorpions *Androctonus australis* (L.) and *Buthus occitanus* (Am.) not only find motionless prey again which was stung but managed to escape before dying: They also respond to extracts of the cuticle of prey insects. After touching prey marks either with the tips of the chelae fingers or the tarsi of the walking legs or the pectine organs specific responses (searching, seizing, feeding) are released at a high rate. Behavioral experiments demonstrate for the first time the chemosensitivity of the pectine organs for which only mechanosensitivity had been proofed formerly. Mechanical as well as contact chemical stimulation of these organs cause scorpions to orient towards the stimulus source which is grasped, retained and consumed or rejected depending on its quality. The probably responsible chemosensitive receptors are already described in the literature. The possible adaptive value and the biological significance of contact chemoreception in prey catching and in other aspects of the life of scorpions is discussed.

I. Introduction

Most of the known scorpion species are assumed to be nocturnal sit-and-wait predators. Mechanical stimuli caused by prey release the capture behavior with its characteristic motor sequences (Le Berre 1979). Substrate vibrations stimulating basitarsal slit sense organs and tarsal hairs direct the vaejovid scorpion *Paruroctonus mesaensis* to its prey which dwells in the sand up to 50 cm away from the predator (Brownell and Farley 1979). In the nearfield the trichobothria serving as sensitive air movement detectors (Hoffmann 1967) restricted to the pedipalps in scorpions, register prey-generated air vibrations and release exactly oriented catching actions (Krapf in prep.).

Detection of motionless or dead prey by scorpions has been rarely described in the literature (Pocock 1893, Rosin and Shulov 1963, Stahnke 1966) and seems to play no essential role in prey acquisition, according to general opinion.

Regarding observations on *Androctonus australis* (L.) and *Buthus occitanus* (Am.) in the laboratory, this kind of foraging might be of greater importance than

has been assumed up to now. At least under laboratory conditions it could often be observed that scorpions, in some cases even before direct contact, perceived dead insects, grasped them after brief searching movements and ate them up.

Concerning their surface activities and hunting strategy, *Androctonus australis* and *Buthus occitanus* seem to resemble *Centruroides sculpturatus*, which far away from its shelter, actively pursues insects in its desert habitat in North America (Hadley and Williams 1968).

The aim of this study is to answer the question whether prey items not sending out any mechanical stimuli detectable from a distance can be perceived by scorpions. Since the optical sense seems to play no role in identifying prey, it was natural to presume that the perception of chemical cues could be decisive.

Hardly anything is known about the chemical sense in scorpions (for references, s. Root 1986). As shown by Foelix and Schabronath (1983) and Foelix and Müller-Vorholt (1983) these arachnids possess sensilla which — regarding their fine structure — can be classified as contact chemoreceptors.

II. Materials and Techniques

Androctonus australis and *Buthus occitanus* caught in their natural habitats in South Tunisia were kept singly in the laboratory on sand in plastic containers with 20 × 20 × 10 cm. The experiments were performed in the containers in a dark room during daytime under red light illumination. The trials were recorded on video tape. The temperature was kept constant at 25 degrees Celsius. The scorpions were starved at least one week before testing. Prey insects were laboratory bred house crickets (*Acheta domesticus*) and larvae of the argentine tenebrionid beetle *Zophobas morio*. The insects were killed by deepfreezing.

To elicit prey catching behavior by airborne vibrations a vibrating ball of cork (10 mm diameter) driven by a frequency generator was held about 2 cm away from the scorpion's pedipalps. The vibration frequency was varied from 1 to 80 Hertz, the amplitude from 0.5 to 3 mm.

To test the extracts, cylinders of plotting paper (15 mm length, 2 mm diameter) were used as dummies. 50 half-grown larvae of *Zophobas morio* were stirred in 50 ml cold dichlormethane for 1 hour (this procedure makes the extraction of substances from interior tissues very unlikely; Peschke, pers. comm.). The surface extract of the cuticles was evaporated to 2.5 ml. 50 μl were dropped onto each dummy (this was equivalent to one larva) and the same amount of pure solvent onto each control. Thereafter, the dummies were dried for 1 hour. Both the dummies and the dead prey were presented on the surface of the sand in a random order.

The behavior of the scorpions after contacting the targets was recorded (for evaluation only directly observed contacts with the extremities were considered).

As positive responses one or more of the following behavioral patterns was classified: 1. orientational movement to the stimulus source, 2. touching of the ground with the tips of the chelae fingers (this remarkable behavior is rarely to be observed in hunting scorpions except in search for prey), 3. digging, 4. grasping the prey or dummy, 5. retaining the prey for at least 20 seconds within the chelae, 6. stinging to kill the prey and feeding attempts. The occurrence of 1. escape, 2. striking for defense with the tail, 3. cleaning and 4. lack of any visible reaction were categorized as negative responses.

In order to test the difference between a mechanical contact stimulus and an additional chemical stimulus applied to the tips of the chelae fingers and the pectine organs, respectively, some larvae of *Zophobas morio* were killed and eviscerated; the cuticles were extracted in the Soxhlett extractor in dichlormethane for 6 hours and dried for 24 hours

afterwards. The responses to cut-out pieces of the extracted cuticles were compared to those of freshly killed larvae.

Results of trials with *Androctonus australis* and *Buthus occitanus* were pooled as there were no recognizable differences in the behavior investigated.

The statistical significance of the results was tested by the 2×2 contingency table and the chi-square test (SACHS 1984).

III. Results

What makes a scorpion search the substrate for a motionless prey?

Under experimental conditions prey catching behavior in buthid scorpions may easily be released by airborne vibrations or immediate contact with the prey. They often pursue a moving stimulus source and try to grasp it.

60 scorpions were stimulated either by airborne vibrations about 2 cm away from the pedipalps or by slightly touching the tips of the chelae fingers with an insect. Fig. 1 shows that these stimuli release the prey capture with high probability (significant differences between positive and negative responses, $P < 0.001$ and $P < 0.01$). Only a few animals withdraw, strike for defense with their tail or show no response at all.

If a scorpion being highly motivated for catching prey, is prevented from successfully grasping the stimulus source by quickly removing it the following behavior can often be observed: 1. oscillating of the pedipalps in the air. In oscillating, *Buthus occitanus* ($N = 4$) moves both pedipalps simultaneously back and forth, with frequencies between 4 to 17 Hertz; hereby, the angle between the tips of the chelae and the chelicerae shifted from 37 to 92 degrees (normal angle between pedipalps in hunting: about 80 degrees). These rhythmic oscillations increase the
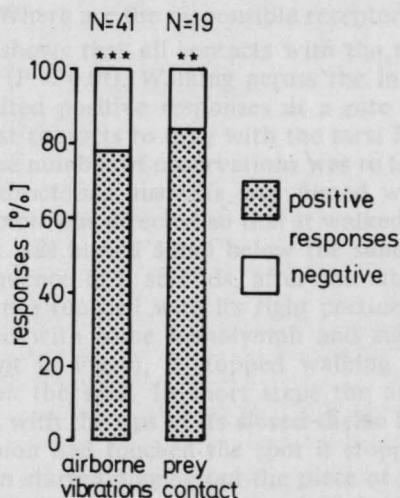

Fig. 1. Occurrence of positive and negative responses of scorpions which were stimulated to prey catching behavior by airborne vibrations (left) and direct prey contact (right).

For the definition of positive and negative responses, see text. For all figures, N denotes the numbers of individuals tested; the number on top of the columns is the number of trials. Level of statistical significance: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

probability to get into contact with prey sitting in the scorpion's close range. 2. Tripping upon the substrate with the first pair of legs, 3. intense movements of the pectine organs which are touching the surface and deepenings of the substrate.

In animals showing one or more of these behavioral patterns the ability was tested to discover chemical cues on substrate and to respond to them. If the responses of hunting scorpions ($N = 9$) are analyzed the first contacts with dead prey or with dummies with extracts of prey both lying on the substrate released searching to 88% ($n = 16$). Hence, activating scorpions by airborne vibrations or by contact with prey not only releases the catching behavior, but also makes them more sensitive to chemical cues on substrate.

Responses to dead prey in scorpions which were not stimulated anyhow before were sporadically observed in animals just caught in the field and put into containers. In those which were starved for a longer time (> 2 months) and in freshly molted ones the readiness to take up dead prey or prey remains was raised, too. Starvation might therefore lower the threshold to search for dead prey in the field.

Perceiving dead prey

Freshly killed half-grown *Acheta domesticus* and *Zophobas* larvae were placed onto the sand with their ventral side down. Fig. 2 a shows the responses of scorpions which happened upon dead insects. In 90% of trials ($n = 49$) positive responses were released. The scorpions seized the dead prey and always started eating it (the difference to the negative responses was highly significant, $P <$ 0.001).
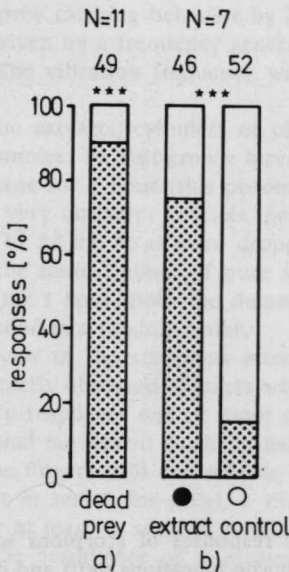

Fig. 2. Occurrence of positive and negative responses to prey marks lying on the surface of the substrate
a) responses to dead prey insects, b) responses to dummies with extracts of the cuticle of prey insects (black circle) and to control dummies (white circle) with solvent applied

Observations on *Buthus* which were fed with *Gryllus bimaculatus* suggest the possible biological function of the behavior described above. Although the crickets were immediately stung by the scorpions and first signs of poisoning became obvious about three seconds later, some of the crickets managed to jump away after autotomy of one hind leg. Other crickets were experimentally removed from the scorpions' chelae and hidden in the containers about 10 cm away from the predator. In this situation all of the 9 scorpions observed started to search for the missing prey and regained the poisoned insects in 3 minutes at most.

In contrast to their first encounter with the living prey the scorpions seized the motionless crickets without any haste and did not sting for a second time. The behavior of these scorpions demonstrates that after stinging they search for escaped prey in the proximity expecting lack of mechanical stimuli conducted by air or substrate.

The importance of an effective sting in regaining lost prey is demonstrated in the following experiment. 31 scorpions were fed with a house cricket each, all of which were stung. Only 2 (= 6%) of the insects escaped thereafter, but were regained by the scorpions after searching for about 4 minutes. In an additional trial, 24 scorpions got crickets, too, but the penetration of the stinger into the prey was prevented by a piece of cork, screening the insect. Here, 42% of the crickets managed to jump away almost unhurt. None of them was found by the searching scorpions (the differences in comparing the responses of both trials are highly significant, $P < 0.01$).

In situations were prey items escaped before they were stung the scorpions showed quite a different behavior compared to the situation described above: when scorpions came across the insects for a second time they rapidly grasped and stung them — even if the victim had remained motionless.

Where are the responsible receptors localized?

Fig. 3. shows that all contacts with the tips of the chelae fingers led to seizing the prey ($P < 0.01$). Walking across the insects and touching them with the pectines elicited positive responses at a rate of more than 80% ($P < 0.05$ and $P < 0.01$). First contacts to prey with the tarsi II to IV were eliciting, too, but for evaluation the number of observations was to low.

An *Androctonus australis* was filmed which pursued an air vibrating source. The scorpion was directed so that it walked over a spot where a piece of a *Zophobas* larva was buried 5 mm below the sand surface. Fig. 4 shows the tracing of a video sequence of 9 seconds, after the vibrational stimulus was removed. When *Androctonus* touched with its right pectine a loamy substrate particle which was besmeared with some hemolymph and substances from the cuticle (= contaminated spot in Fig. 4), it stopped walking at once, oscillated the pedipalps and tripped on the spot. In short steps the animal walked backwards touching the substrate with the tips of its closed chelae fingers in search for the stimulus. After the scorpion had touched the spot it stopped walking, picked its chelae into the sand, then started digging out the piece of larva, grasped it and ate it up.

Which properties of motionless prey are perceived by scorpions?

As scorpions responded to freshly dead insects the question was whether they perceive mechanical or chemical properties of motionless prey. To exclude that the scorpions predominantly respond to mechanical properties of the insect cuticle the influence of chemical cues was tested. Therefore the scorpions were offered on the one hand dummies impregnated by extracts from larvae cuticles and on the other hand dummies with only solvent applied.
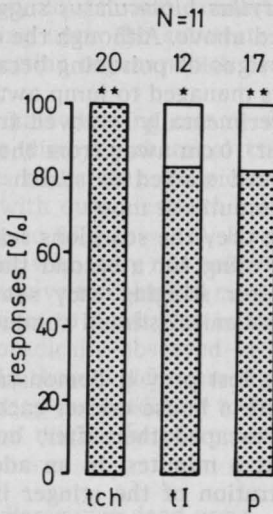
Fig. 3. Occurrence of positive and negative responses of scorpions coming across dead prey insects lying on the substrate. The scorpions had touched them either with the tips of the chelae fingers (tch) or the tarsi of the first walking legs (tI) or the pectines (p)
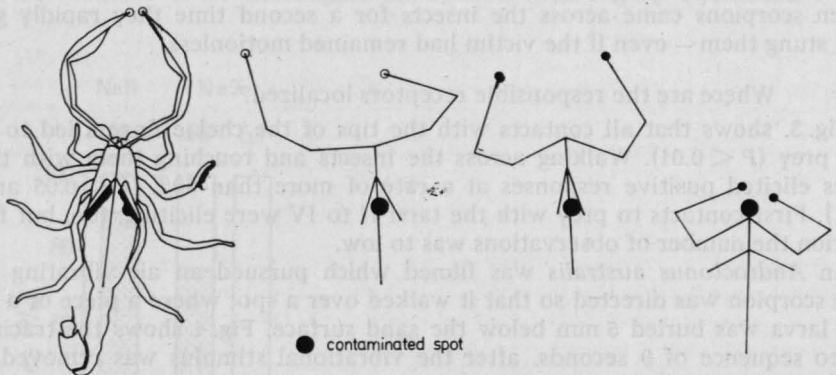

Fig. 4. *Androctonus australis* touching with the right pectine substrate particles besmeared with prey remains (contamined spot). White circle on the tip of chelae: chela without contact to substrate. Black circle: finger tip of chela touches the ground for search. Tracing of a video sequence

Comparable results are obtained as in the experiments concerning recognition of dead prey: dummies with extracts were significantly preferred to the controls ($P < 0.001$; Fig. 2 b). The dummies elicited positive responses in 67% to 92% of all cases (Fig. 5), when the scorpions touched them either with the finger tips or the tarsi of the first walking legs or the pectine organs. The dummies were partly handled like prey animals, i.e. they were retained, sometimes stung and also treated as food. In eight cases of positive response to controls these were seized only two times and brought to the mouthparts. Control dummies usually released only a brief touch with the finger tips or a brief grasp with a chela.

In order to answer the question whether a scorpion shows different responses when it is actively touched, either with an intact insect or with an insect, whose contact chemical identification should have been rendered more difficult by extracting chemical compounds from the cuticle, the following experiments were carried out.
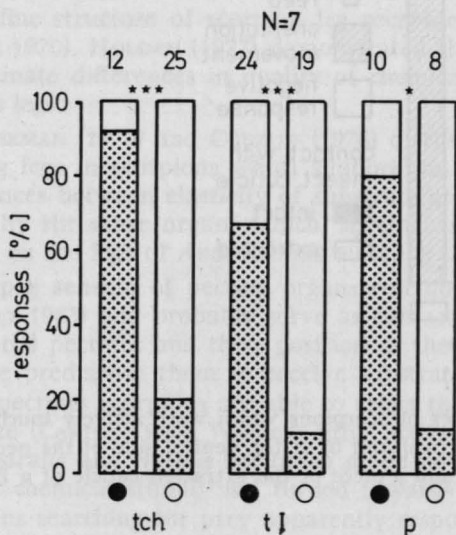

Fig. 5. Occurrence of positive and negative responses of scorpions coming across dummies with extracts of prey insects (black circle) and control dummies with solvent applied (white circle). The scorpions had touched them either with the tips of the chelae fingers (tch) or the tarsi of the first walking legs (tI) or the pectines (p)

5 scorpions were touched at the tips of the chelae fingers with 1. a dead Zophobas larva and 2. a piece of the extracted cuticle of a Zophobas larva.

The intact larvae were very attractive to the scorpions and were grasped at once to 96% (Fig. 6 a). In these cases of positive response they nearly always retained the prey and ate it up. The controls (extracted larva cuticle) elicited grasp response in 78% of cases, which is (with $P < 0.01$) a significant difference to the result obtained in the former trial. Intense responses (retaining and feeding attempts) to the controls followed the grasping in only 22% of cases.

In a corresponding experiment the pectine organs were tested. Through vibrational or tactile stimulation scorpions were caused to assume body postures allowing the ventral side of the pectines to be touched. Orientation movements towards the stimulus source were considered a positive response here. Since such movements could be only observed upon direct contact with the pectines the participation of other receptors (e.g. the trichobothria) in releasing this response can be excluded. As shown in Fig. 6 b, both intact larvae and pieces of extracted larva cuticle induced orientation movements in about 90% of cases (the difference is not significant, $P > 0.05$). When the scorpions had the possibility of grasping the targets they showed responses as already demonstrated in Fig. 6 a.
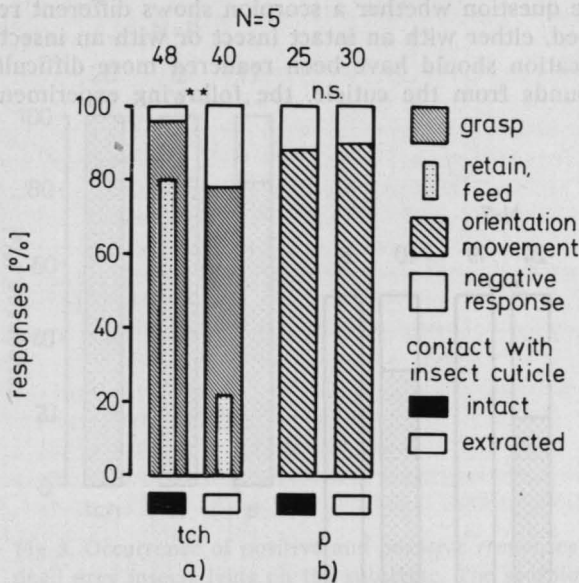
Fig. 6. Occurrence of responses of scorpions which were actively touched a) at the tips of the chelae fingers (tch) and b) at the ventral side of the pectines (p) with a dead Zophobas larva and a piece of the extracted cuticle of a Zophobas larva

IV. Discussion

As the results show, scorpions are able to find prey which does not betray itself by movements. Androctonus australis and Buthus occitanus are not exclusively sit-and-wait predators remaining all the time near the entrance of their burrow — as many other scorpion species do — but prowl around for prey and even climb up vegetation. Although it is very unlikely that these predators often come across dead prey by chance, they should utilize it at every turn — especially under the scanty conditions of desert life (POLIS 1980 a).

The main value of the abilities described above must probably be seen in quite a different connection. Buthid scorpions are capable of catching highly mobile prey like cockroaches, crickets and even flying insects, which normally are stung immediately after seizing. Nevertheless, some prey items still manage to escape, but die quickly in the close range of the predator. Field observations suggest a low hunting success of Androctonus australis and Buthus occitanus because prey is normally scattered making encounters a rare event. Therefore, searching in the surroundings for probably hurt or died prey should be more profitable to the predator than investing much time and energy in hunting living and mobile prey.

Chemical compounds of the surface of the prey cuticle seem to be adequate stimuli for receptors which are known from all appendages of scorpions. Hair sensilla on the distal segments of the legs the fine structure of which had been described by FOELIX and SCHABRONATH (1983) in Androctonus australis and Buthus occitanus could be responsible for the recognition of chemical prey cues. Multiply innervated mechano- and chemoreceptors are densely arranged on the ventral side of tarsi and basitarsi especially of the first walking legs. The authors classi-

fied short hairs with an opening in the blunt tip, curved downwards to the ground as chemoreceptors. This points to the function of these hairs in tasting chemical properties of prey items on the substrate. Supports for this assumption are the electrophysiological responses to contact stimulation of leg hairs of this type by chemicals in the spider *Ciniflo* (HARRIS and MILL 1977). The large number of 19 chemoreceptor cells per sensillum is discussed as a possibility to identify specifically characteristic substances, including those from potential prey.

The fine structure of scorpion leg receptors is very similar to that of spiders (FOELIX 1970). HOLDEN (1977) demonstrated that *Araneus diadematus* was able to discriminate differences in quality of chemically treated flies after short contact with its legs.

BOWERMAN (1975) and COUZIJN (1976) discussed the possible importance of first walking legs in scorpions which support the sensory functions of the pedipalps. Differences between elasticity of substrate and contacted prey could also be perceived by slit sense organs which, serving as strain gauges, are numerously arranged on the legs of *Androctonus australis* (BARTH and WADEPUHL 1975).

The peg sensilla of pectine organs resemble tarsal hairs (FOELIX and MÜLLER-VORHOLT 1983) and probably serve as contact chemoreceptors as well. The mobility of the pectines and their position at the ventral side of the scorpion's body likewise predispose them to receive substrate bound informations. With the aid of the pectines scorpions are able to select the substrate with their preferred particle size (CARTHY 1966). Whereas after actively contacting the pectines *Androctonus australis* and *Buthus occitanus* made no difference between mechanical and contact chemical stimuli and turned towards the stimulus source in both cases, scorpions searching for prey apparently responded preferred to chemical cues on substrate which were touched with the combs. Comparable responses were lacking when the scorpions came across the rough ground, touching with the pectines stones etc. sticking out of the surface. Although the results ascribe a part to the pectine organs in prey recognition and prey finding this is probably only one of many other functions which must be considered. The biological meaning of the noticeable variations in the number of pectinal teeth when comparing the sexes or species as well as the correlation between the number of pectinal teeth and parameters of the habitat (SREENIVASA-REDDY 1959) have never been studied in detail.

Receptors on the pedipalps are determinative in food selection. Sensilla on the tips of the chelae fingers apparently have influence on the scorpion's decision between "keep on searching; retain" and "reject it". Concerning the morphology of the fields of hair receptors and their position at the distal part of the chelae (IVANOV 1981), contact chemoreception is very likely in these receptors. These receptor fields are not as contrasting in scorpionids as in the slender-armed buthids. Nevertheless, *Pandinus imperator* was observed to examine a spot with its chelae, where a diplopod had been killed and eaten by a conspecific. At least in some actively foraging buthid species it is likely that the pursuit of chemical trails of prey items guides these predators to the most suitable chasing area.

As already mentioned above the chemical sense in scorpions is poorly investigated but some observations hint to its role in sexual behavior. For example, in *Pandinus imperator* an adult male started juddering the whole body when it walked across a piece of bark originating from a female's container (to bark of its own container it showed no comparable movements). This points to a contact chemical perception of female sex pheromones, eliciting prenuptial behavior in the male scorpion.

VANNINI and UGOLINI (1980) recorded contact chemoreception in the binding of mother and larvae of *Euscorpius carpathicus*. The larvae prefer substrate contaminated with extracts of the cuticle of conspecifics and that of other scorpion species as well compared to a neutral ground. To the juveniles the recognition of the scorpion's cuticle secures the stay on the mother's back where they spend the critical time in safety up to the first molt.

Observations on own laboratory breds of *Heterometrus spinifer* have confirmed NEMENZ and GRUBER (1967): nearly 30 one-year-old scorpions gathered at a dead *Periplaneta americana*, dragged it to their shelter, cut it into pieces and ate it up together. Cannibalism, a common behavior in many scorpion species (POLIS 1980 b), was never observed despite the crowding. In this case the important function of chemoreception might be to discriminate prey and conspecifics.

Acknowledgements

Zusammenfassung

Skorpione werden im allgemeinen für Räuber gehalten. Im Labor reagieren die Buthiden *Androctonus australis* (L.) und *Buthus occitanus* (Am.) jedoch auch sehr empfindlich auf tote, am Boden liegende Insekten. In vielen Fällen wird die regungslose Beute ergriffen und gefressen. Die vorliegende Arbeit untersucht, wie dieses Verhalten experimentell ausgelöst werden kann.

Die Ergebnisse zeigen, daß *Androctonus* und *Buthus* nicht nur bewegungslose Beute wiederfinden, welche ihnen nach dem Stich entkommen war und dann starb; sie reagieren auch auf Oberflächenextrakte der Kutikula von Beuteinsekten. Die Berührung extraktbehandelter Attrappen löst — im Vergleich zu neutralen Kontrollen — in hohem Maß spezifische Verhaltensweisen aus (Suchen, Zugreifen, Fressen).

Nach den Beobachtungen liegen die für die Wahrnehmung verantwortlichen Rezeptorsysteme an den Spitzen der Scherenfinger, an den Tarsen der Laufbeine und auf den Kammorganen. Zum ersten Mal wird im Verhaltensversuch für die Kammorgane Chemosensibilität nachgewiesen; ihre Bedeutung als Aufnehmer mechanischer Reize ist schon länger bekannt. Nach mechanischen und kontaktchemischen Reizen an den Kämmen zeigen die Skorpione Orientierungsbewegungen zur Reizquelle hin und ergreifen diese. Je nach deren Beschaffenheit wird sie festgehalten und gefressen oder abgelehnt. Die Verhaltensexperimente legen nahe, daß in der Literatur beschriebene chemosensitive Rezeptoren an den Extremitäten die chemische Information der Beute vermitteln.

Der mögliche Anpassungswert für den Beutefang sowie mögliche biologische Bedeutungen von Kontaktchemorezeption im Leben der Skorpione werden diskutiert.

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