

## Is *Tityus uruguayensis* (Buthidae) an araneophagic scorpion? An experimental analysis of its predatory behaviour on spiders and insects

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### Summary

The predatory behaviour of the buthid scorpion *Tityus uruguayensis* Borelli was studied under laboratory conditions. Six types of prey of the same size — three types of insects and three of spiders — were offered to juvenile and adult female scorpions. The insects used in experiments were cockroaches, mealworm larvae and crickets; the spiders were lycosids, amphinectids and dysderids. The scorpions were found to be mainly araneophagic, attempting to capture all the spider types, whereas the crickets were the only insects attacked. Scorpions always tried to sting the prey and frequently released them after stinging. Dysderid spiders were rarely captured, showing an effective anti-predatory display which consisted of opening their large fangs. Other spiders attempted to escape or performed leg autotomy as their main defensive behaviours. Stung prey died quickly and scorpions located the prey and dragged and carried them before ingestion. Sagittal and lateral tail movements were observed after capture. The results clearly suggest a preference of this species for spiders, although crickets were also attacked. Scorpions recognised the non-native and well-armed *Dysdera crocata* as a spider, but failed to capture it. Scorpion poison seems to be very effective, in agreement with the observed tactic “sting-and-release” of the prey.

### Introduction

Scorpions are polyphagous predators with a wide food range, from annelids to small vertebrates (Stahnke, 1966; Casper, 1985; Polis, 1990). Literature on this topic is abundant but mainly anecdotal, reporting casual findings in the field or data from scorpion breeding under laboratory conditions. More precise studies on the feeding behaviour of some scorpions were carried out by Schultze (1927), Baerg (1954), Main (1956), Cekalovic (1967), Hadley & Williams (1968), Alexander (1972), Lourenço (1976), Eastwood (1978), Harington (1978), Polis (1979), Bub & Bowerman (1979), Cushing & Matherne (1980), McCormick & Polis (1982), Shachak & Brand (1983), Polis & McCormick (1986), and Polis (1990). These authors analysed species of Bothriuridae, Scorpionidae and Vaejovidae. Not unexpectedly, the most common scorpion prey are listed as insects, arachnids and myriapods. The available literature about the prey of species of buthid scorpions is listed in Tables 1 and 2, which also show a wide range of potential prey. Le Berre (1979) and recently Rein (2003),

have studied particularly the prey capture behaviour of buthid scorpions.

*Tityus uruguayensis* Borelli 1901 (Fig. 1) is a small Neotropical buthid (approximately 5 cm in body length) which inhabits Uruguay, the south of Rio Grande do Sul State, Brazil, and Entre Rios Province, Argentina (Lourenço & Maury, 1985). Its food preferences are poorly known: San Martín (1961), Zolessi (1985) and Toscano-Gadea (2001) stated that under laboratory conditions this species eats only flies, crickets, spiders and pieces of mealworms (Table 1). The first author of the current paper has reared several specimens, feeding them mainly with spiders, because they often rejected entire mealworms or cockroaches, which are frequently used as prey in the laboratory. Potential prey of *T. uruguayensis*, such as cockroaches, crickets, grasshoppers, insect larvae and spiders, were found co-occurring with this scorpion in pitfall traps in three localities near Montevideo (Pérez-Miles *et al.*, 1999; Toscano-Gadea, 2002; Pérez-Miles *et al.*, 2005).

Taking into account this background, we tested the hypothesis that *T. uruguayensis* is mainly araneophagic by experimentally studying the prey-capture success of the scorpion on three types of insects and three types of spiders. The results provide the first knowledge of prey preferences in this buthid species.

### Methods

Two categories of scorpion individuals were used: adults and juveniles. Adults were collected as pregnant females at Estación Trinidad and Puntas de Cuñapirú, two neighbouring localities in the Department of Rivera, northern Uruguay (approximately 31°03'S, 55°37'W). All juveniles used were broods from these females and had moulted twice after birth (*T. uruguayensis* reaches maturity after 5 moults according to Zolessi, 1985). Adults were housed in individual glass jars of 9 cm diameter; juveniles were kept in individual small petri dishes of 4 cm diameter. In both cases, we used damp sand as a substrate and source of water. During the whole period of study (from November 2001 to October 2002), they were fed with assorted living spiders (mainly lycosids and amphinectids) and pieces of mealworm larvae. Room temperature averaged 22.4°C ( $\pm$  2.6 SD, range: 12–30).

The prey used in all the experiments had approximately the same weight as the scorpion individuals (see Table 3). The insects used were: cockroaches *Blaptica dubia* (Serville, 1839) (Blaberidae), mealworm larvae *Tenebrio molitor* (L.) (Tenebrionidae) and crickets (*Eugrylloides* sp., *Pteronemobius* sp. and *Argizala* sp.). Spiders were: lycosids (*Schizocosa malitiosa* (Tullgren), *Lycosa thorelli* (Keyserling) and *L. carbonelli* Costa & Capocasale), amphinectids (*Metaltella simoni* (Keyserling), a cribellate web builder), and dysderids (*Dysdera crocata* C. L. Koch).

For the experiments, scorpions were placed into petri dishes of 8.7 cm diameter and 1.4 cm height for adult females, and 3.4 cm diameter and 0.9 cm height for juveniles. The volume of the petri dishes for adult

Scorpion species	Prey used	Reference
<i>Amanteris coineai</i> Lourenço, 1982	Crickets and spiders	Lourenço & Cuellar, 1999
<i>Buthus occitanus israelis</i> Shulov & Amitai, 1959	Arachnids, cockroaches, moths, beetles, Neuroptera and termites: <i>Anacanthotermes</i> sp.	Skutelsky, 1995, 1996
<i>Centruroides gracilis</i> (Latreille, 1804)	<i>Periplaneta americana</i> , <i>P. australasiae</i> , <i>Blattella germanica</i> and <i>Pycnocellus surinamensis</i> (Dictyoptera)	Teruel, 2004
<i>Centruroides insulanus</i> Thorell, 1877	Crickets, cockroaches, grasshoppers, and <i>Tenebrio</i> sp. larvae (Coleoptera)	Baerg, 1954
<i>Isometrus (R.) besucheti</i> Vachon, 1982	Crickets, spiders and <i>Tenebrio</i> sp. larvae (Coleoptera)	Huber <i>et al.</i> , 2002
<i>Isometrus (I.) maculatus</i> (De Geer, 1778)	Crickets, spiders and <i>Tenebrio</i> sp. larvae (Coleoptera)	Huber <i>et al.</i> , 2002
<i>Isometroides vescus</i> Karsch, 1880	Spiders: Theridiidae	Main, 1956
<i>Parabuthus leiosoma</i> (Ehrenberg, 1828) and <i>P. pallidus</i> Pocock, 1895	<i>Tenebrio molitor</i> larvae (Coleoptera) and <i>Lithobius forficatus</i> (Centipede)	Rein, 2003
<i>Tityus fasciolatus</i> Pessoa, 1935	Grasshoppers, termites, cockroaches and <i>Tenebrio</i> sp. larvae (Coleoptera)	Britto-Knox, 1997
<i>Tityus metuendus</i> Pocock, 1897	Crickets and spiders	Lourenço & Cuellar, 1999
<i>Tityus serrulatus</i> Lutz & Mello, 1922	Grasshoppers, termites, cockroaches and <i>Tenebrio</i> sp. larvae (Coleoptera)	Britto-Knox, 1997
<i>Tityus serrulatus</i> Lutz & Mello, 1922	<i>Gryllus</i> sp. (Orthoptera), <i>Periplaneta americana</i> and <i>Pycnocellus</i> sp. (Dictyoptera)	Candido & Lucas, 2004
<i>Tityus uruguayensis</i> Borelli, 1901	<i>Musca</i> sp. (Diptera)	San Martin, 1961
<i>Tityus uruguayensis</i> Borelli, 1901	<i>Drosophila</i> sp., <i>Musca</i> sp. (Diptera) and crickets	Zolessi, 1985
<i>Tityus uruguayensis</i> Borelli, 1901	Spiders ( <i>Selenops</i> sp., <i>Lycosa</i> sp., <i>Metaltella</i> sp.) and <i>Tenebrio</i> sp. larvae (Coleoptera)	Toscano-Gadea, 2001
<i>Uroplectes lineatus</i> C. L. Koch, 1844	Isopods, beetles and mealworms	Eastwood, 1978

Table 1: List of reported prey of buthid scorpions in laboratory conditions.

scorpions was approximately ten times that of the petri dishes for juvenile scorpions, maintaining the same ratio observed between the weights of these scorpions (Table 3). The cover of each petri dish had a central hole (1 cm diameter), allowing us to introduce the prey without disturbing the scorpion. This hole was closed with a plug. Scorpions were deprived of food for at least one week before the experiments. Compressed humid soil was used as substrate. The soil was renewed before

the introduction of new scorpions, which were weighed and replaced 24–72 h before the introduction of prey. Prey were weighed immediately before the experiments. When the prey was introduced, interactions were directly recorded and timed: each experiment took 15 min following the first contact between both animals. Two consecutive series of experiments were carried out using the same scorpions, with at least one month interval between them. In the first series, captured

Scorpion species	Prey used	Reference
<i>Alayotityus delacruzii</i> Armas, 1973	<i>Cubacubana decui</i> (Thysanura)	Teruel, 1997
<i>Alayotityus delacruzii</i> Armas, 1973	Blattidae (Dictyoptera), Nicolettidae (Thysanura) and Tenebrionidae (Coleoptera)	Teruel, 1997, 2001
<i>Alayotityus juraguensis</i> Armas, 1973	<i>Rhytidoporus identatus</i> (Heteroptera)	Teruel, 1997
<i>Alayotityus nanus</i> (Karsch, 1879)	Diplopods (Myriapoda)	Teruel, 1996
<i>Alayotityus nanus</i> (Karsch, 1879)	<i>Odontomachus</i> sp. (Formicidae)	Teruel, 1996
<i>Alayotityus nanus</i> (Karsch, 1879)	Geophylomorpha (Chilopoda)	Teruel, 1997
<i>Alayotityus sierramaestrae</i> Armas, 1973	<i>Pycnoscellus surinamensis</i> (Dictyoptera: Blattidae)	Teruel, 1997
<i>Buthus occitanus</i> (Amoreaux, 1789)	Ants ( <i>Messor</i> sp.), beetles and <i>Mauremys leprosa</i> (Chelonia)	Bejarano & Pérez-Bote, 2002
<i>Buthus occitanus israelis</i> Shulov & Amitai, 1959	Arachnids, cockroaches, moths, beetles, Neuroptera and termites: <i>Anacanthotermes</i> sp.	Skutelsky, 1995, 1996
<i>Centruroides anchorellus</i> Armas, 1976	<i>Apis mellifera</i> (Hymenoptera: Apidae)	Teruel, 1997
<i>Centruroides arctimanus</i> Armas, 1973	Blattidae (Dictyoptera)	Teruel, 1996
<i>Centruroides gracilis</i> (Latreille, 1804)	<i>Periplaneta australasiae</i> (Dictyoptera: Blattidae) and <i>Scolopendra</i> sp. (Chilopoda)	Teruel, 1997
<i>Centruroides gracilis</i> (Latreille, 1804)	<i>Anolis porcatu</i> s (Squamata: Polychrotidae)	Armas, 2001
<i>Isometroides vescus</i> (Karsch, 1880)	Spiders: Mygalomorphae and Lycosidae	Main, 1956
<i>Rhopalurus garridoi</i> Armas, 1974	<i>Byrsotria</i> sp. (Dictyoptera)	Teruel & Diaz, 2002
<i>Rhopalurus junceus</i> (Herbst, 1800)	<i>Byrsotria</i> sp. (Dictyoptera), <i>Heteropoda venatoria</i> (Araneae) and Mygalomorphae	Teruel, 1996, 1997
<i>Rhopalurus junceus</i> (Herbst, 1800)	<i>Sphaerodactylus elegans</i> (Squamata: Gekkonidae)	Armas, 2001
<i>Rhopalurus princeps</i> (Karsch, 1879)	<i>Ameiva lineata</i> (Squamata: Teiidae)	Armas, 2001
<i>Tityus obtusus</i> (Karsch, 1879)	<i>Eleutherodactylus coqui</i> (Anura: Leptodactylidae)	Armas, 2001
<i>Tityus quisqueyanus</i> Armas, 1981	<i>Eleutherodactylus patriciae</i> (Anura: Leptodactylidae)	Armas, 2001
<i>Tityus trivittatus</i> Kraepelin, 1898	Spiders and cockroaches	Mauy, 1997
<i>Uroplectes otjimbinguensis</i> (Karsch, 1879)	<i>Gandanameno echinatus</i> (Araneae: Eresidae)	Polis, 2001

Table 2: List of reported prey of buthid scorpions in field conditions.

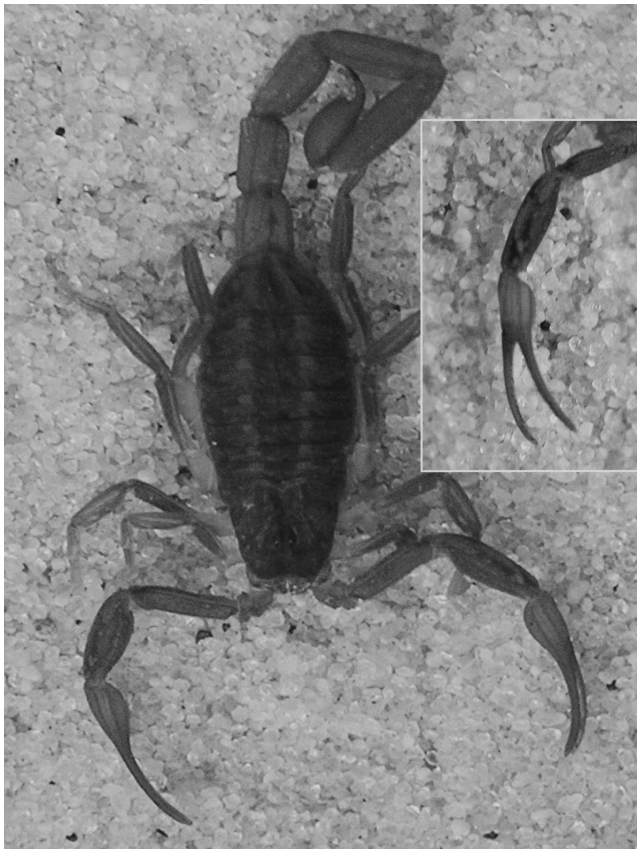


Fig. 1: Adult female of *Tityus uruguayensis* and detail of one slender pedipalp. Photograph by Gonzalo Useta.

prey were removed (to avoid the food influencing the scorpions for the second series); in the second series, the scorpions were allowed to eat the prey. Each scorpion was confronted with two different types of prey (one insect and one spider, which were randomly assigned). Twenty-four adult females and 72 juveniles were used for each series, totalling 48 and 144 experiments, respectively.

Room temperature during the first series averaged  $22.0^{\circ}\text{C}$  ( $\pm 0.02$  SD) for the adults and  $21.9^{\circ}\text{C}$  ( $\pm 0.2$ , range: 21.5–22.0) for the juveniles; during the second series it averaged  $21.0$  ( $\pm 1.0$  SD, range: 20.0–22.0) for the adults and  $22.7$  ( $\pm 0.75$  SD, range: 22.0–24.0) for the juveniles.

Chi-square tests for one, two and multiple independent samples, ANOVA, Kruskal–Wallis tests and regression lines, were used for statistical analysis.

## Results

### *Scorpion predatory behaviour*

During the prey–predator encounters, fourteen behavioural units for the scorpions were recognised. Cleaning movements using the mouthparts were sporadically observed, but were not quantified.

- (1) *Alert*: The scorpion extends its pedipalps forwards, opens the chelae and raises the tail (initially curved) from the horizontal to the vertical position (sagittal plane).

- (2) *Orientation*: In the same position as Alert, the scorpion orientates itself towards the moving prey.
- (3) *Grasp attempt*: The scorpion moves to the prey and attempts to grasp it with its pedipalps.
- (4) *Sagittal tail oscillations*: Oscillations of the lifted tail with alternating rapid and discontinuous forward movements and slow backward movements in the sagittal plane, ending in a final forward movement of the telson (until it reaches the cheliceral level). This may occur before or after prey capture.
- (5) *Lateral tail oscillations*: Slow oscillations of the lifted tail in the transverse plane, at variable amplitude. This behaviour may be performed before or after prey capture.
- (6) *Rejection tail movements*: The scorpion orientates itself in relation to the prey with the tail curved laterally, and knocks the prey horizontally one or more times with the ventral face of the vesicle, driving the prey away.
- (7) *Eating lost prey leg*: The scorpion eats a pulled-off or autotomised leg, and frequently searches for the living prey while eating the leg.
- (8) *Stinging the prey*: First, the scorpion catches the prey with one or two pedipalps, tries to sting in a soft part of the prey, and then extends the tail while maintaining the grasp with one or both pedipalps. Immediately, the scorpion stops stinging and relaxes the tail, keeping the prey as far away as possible grasped by one extended pedipalp. Sometimes, the scorpion repeats the sting.
- (9) *Pseudo-stinging*: While grasping the stung prey, the scorpion softly taps the prey with the dorsal and/or ventral face of the telson, but without stinging it.
- (10) *Wait-and-search for stung prey*: After stinging, the prey may escape or be freed by the scorpion, which remains immobile for some seconds and then apparently searches for the prey with its pedipalps extended and opened, and with the tail raised. If the scorpion pulled legs off the prey, it searched while carrying the legs with the chelicerae or pedipalps.
- (11) *Dragging the prey*: The scorpion briefly drags the stung prey forwards and/or backwards, while grasping it with the pedipalps and/or chelicerae.
- (12) *Carrying the prey*: The scorpion walks forward for some seconds, grasping the stung prey with one or both pedipalps.
- (13) *Drinking body fluid*: Suction on drops of fluid at the wounds of the prey.
- (14) *Eating*: Chewing movements of the chelicerae on the prey.

### *Sequences and success of capture on each prey type*

*Cockroaches*: Adult scorpions were mainly “indifferent” to this prey type, limiting their behaviour to alert and orientation at the beginning of the experiment. Juveniles were more active and attempted to capture or reject the prey, in a few cases. When disturbed,



cockroaches curved their body (ventral flexion) and remained resting on the substrate.

*Mealworms:* Adult scorpions showed only alert behaviour in a few cases. Juveniles were also basically “indifferent”, but attempted to capture the prey in four cases. Mealworms walked continuously, but wriggled when they were grasped.

*Crickets:* Adult scorpions frequently showed alert and orientation, as well as attempting to capture the prey in seven of the eight cases. Only two prey were captured and carried. One cricket was stung once and the other twice, both being eaten head first. Juvenile scorpions showed nearly all the described behaviours. Tail oscillations were observed in six cases, rejection and pseudo-stinging in two cases, and stinging was performed in ten cases (single sting in seven cases, two stings in one case and undetermined (two or more) in the other two cases). Two scorpions stung their prey, freed them, and searched for them later. Eight juveniles carried the prey, and two of them had previously dragged the prey. Nine juveniles started eating at the head of the prey, and the rest started at the abdomen. Five scorpions bit the cricket in various places before eating it. In one case, the scorpion first drank body fluid from a wound on a third leg of the prey. All crickets actively avoided the scorpions by jumping and walking about; they defended themselves by using their hindlegs when grasped by the scorpion.

*Lycosids:* Scorpions frequently attempted to capture wolf spiders, displaying a rich repertoire of behaviours, but the spiders avoided them in several cases owing to their ability to perceive the predator and to escape rapidly. Furthermore, lycosids autotomised legs in nearly half of the cases, distracting the scorpion. In one case a lycosid bit an adult scorpion on one pedipalp, but apparently did not harm it. Usually, a single sting was sufficient to immobilise the spider. Juvenile scorpions, but not the adults, performed tail movements: rejection (two cases), sagittal oscillations (one case) and lateral oscillations (eleven cases). Two adult scorpions dragged the stung prey and three others carried their prey. In juvenile scorpions, these behaviours were rare (two dragged and one carried). Drinking of body fluid before eating was observed in two cases in adult scorpions. Eating a lost prey leg was observed in half of the experiments.

*Amphinectids:* Juvenile scorpions showed all the described behaviours, while sagittal and rejection tail movements, carrying and drinking were not observed in the adult scorpions. These spiders showed low ability for escaping, walking slowly in relation to lycosids but losing legs easily. A single sting was sufficient to immobilise the spider, except for one adult scorpion which stung twice. Only one adult scorpion dragged the captured spider. Juvenile scorpions dragged prey in five cases, carried in twelve and drank fluid in seven cases.

*Dysderids:* These spiders exhibited a typical threat display with their long fangs opened and forelegs raised, and used the second pair of legs for grasping the opponent. The spider could also escape quickly. In three cases, the spider bit a juvenile scorpion (in two cases on the chelae of the pedipalps and in the other one on the tail) but no damage was observed. Only five captures by juvenile scorpions were observed. Most of the behavioural repertoire was observed. Orientation and rejection tail movements were particularly frequent in both adult (six and four cases, respectively) and juvenile scorpions (fifteen and ten cases). Juvenile scorpions also displayed lateral tail movements in four cases. When the spiders were captured, the scorpions dragged the prey in two cases, carried it in four and drank body fluid in two cases.

We compared the overall performance of the scorpions in the first and second series of experiments (Table 4). We did not observe qualitative differences between the behavioural units of these series. Neither did we find significant differences between the series in either capture or capture attempts on insects or spiders using the Chi-square test (captures of insects by adult scorpions  $\chi^2=0$ ,  $p=1$ , and capture attempts  $\chi^2=0$ ,  $p=1$ ; captures of spiders by adults  $\chi^2=0$ ,  $p=1$ , and capture attempts  $\chi^2=0$ ,  $p=1$ ; captures of insects by juvenile scorpions  $\chi^2=1.72$ ,  $p>0.10$  and capture attempts  $\chi^2=0.98$ ,  $p>0.30$ ; captures of spiders by juveniles  $\chi^2=0.54$ ,  $p>0.30$ , and capture attempts  $\chi^2=1.05$ ,  $p>0.30$ ). We therefore grouped the data from the two series for further comparisons.

When we compared the overall efficacy of capture of insects and spiders (Table 5), we found no difference in adult scorpions ( $\chi^2=3.16$ ,  $p=0.076$ ), but a significant difference in juvenile scorpions ( $\chi^2=7.13$ ,  $p=0.0076$ ). When we compared capture attempts on insects and on

	Large prey			<i>n</i>	Small prey			<i>n</i>
	Mean	SD	Range		Mean	SD	Range	
<b>Insects</b>								
Cockroaches	0.24	0.06	0.16–0.34	8	0.04	0.02	0.02–0.09	24
Mealworms	0.16	0.02	0.13–0.20	8	0.03	0.01	0.01–0.04	24
Crickets	0.27	0.09	0.13–0.39	8	0.06	0.03	0.02–0.12	24
<b>Spiders</b>								
Lycosids	0.22	0.05	0.18–0.29	8	0.05	0.01	0.02–0.07	24
Amphinectids	0.17	0.05	0.12–0.25	8	0.04	0.01	0.02–0.06	24
Dysderids	0.13	0.03	0.11–0.19	8	0.03	0.01	0.01–0.05	24
<b>Scorpions</b>	0.27	0.05	0.15–0.37	48	0.03	0.01	0.01–0.05	144

Table 3: Mean weights (g, SD and ranges) of prey (insects and spiders) and predators (scorpions) used in two types of experiments (adult female scorpions on large prey and juvenile scorpions on small prey); *n*=number of experimental individuals.

	First series		Second series	
	Captures	Capture attempts	Captures	Capture attempts
<b>Adult scorpions (n=12)</b>				
Insects	1	3	1	4
Spiders	4	10	4	9
<b>Juvenile scorpions (n=36)</b>				
Insects	8	15	3	10
Spiders	15	33	11	29

Table 4: Effective captures and capture attempts by adult and juvenile scorpions, discriminated by first and second series of experiments on insects and spiders.

spiders, a significant difference was found in both adult ( $\chi^2=10.15, p=0.0014$ ) and juvenile scorpions ( $\chi^2=37.63, p<0.0001$ ).

We found no significant differences in prey capture efficiency ( $\chi^2=0.23, p>0.50$ ) or in capture attempts ( $\chi^2=0.86, p>0.30$ ) when we compared the performance of adult versus juvenile scorpions. When we combined the data sets from adult and juvenile scorpions, significant differences were found between insects and spiders in both capture efficiency ( $\chi^2=11.27, p<0.001$ ) and capture attempts ( $\chi^2=53.77, p<0.001$ ).

Analysing the performance of scorpions on each prey type separately, we found some differences in both insect and spider groups. Cockroaches, mealworms and dysderids were rarely captured by adult and juvenile scorpions combined, while crickets, lycosids and amphinectids were captured more successfully (Fig. 2). However, when we compared capture attempts, dysderids seemed to be initially attractive for scorpions. When we tested capture attempt frequencies for all scorpions, we found differences in insects ( $\chi^2=43.33, p<0.001$ ) but not in spiders ( $\chi^2=0.47, p>0.70$ ). When we tested capture frequencies, we found differences in both insects ( $\chi^2=23.83, p<0.001$ ) and spiders ( $\chi^2=13.75, p<0.01$ ). Using pair-wise comparisons, we found that capture attempts on crickets were different from cockroaches ( $\chi^2=20.16, p<0.001$ ) and from mealworms ( $\chi^2=17.83, p<0.001$ ), but cockroaches and mealworms were similar ( $\chi^2=0$ ). We also found that captures of crickets were different from cockroaches ( $\chi^2=9.65, p<0.01$ ) and from mealworms ( $\chi^2=12.41, p<0.001$ ), but cockroaches and mealworms were similar ( $\chi^2=0$ ). On spiders, captures of dysderids were different from amphinectids ( $\chi^2=11.27, p<0.001$ ) but not from lycosids ( $\chi^2=1.39, p>0.20$ ), and we found no significant differences between lycosids and amphinectids after Bonferroni correction ( $\chi^2=4.04, p>0.02$ ).

Two sets of duration data were analysed: capture duration and poison latency. We considered capture duration to be the time between apparent perception of the prey by the scorpion (which performed mainly alert and orientation behaviours) until the stinging of the prey. Poison latency was recorded from the first stinging to the first attempt at eating by the scorpion. Results are shown in Table 6. Capture durations showed a wide dispersion of values, while poison latency showed less variation compared with capture duration. Considering only captures by juvenile scorpions (because of larger amounts of data) we tested whether there were statistical differences in the two sets of duration data for crickets, lycosids, amphinectids and dysderids. No differences were found either in capture duration (ANOVA:  $F=0.096, p=0.962$ ) or in poison latency (Kruskal–Wallis:  $H=4.812, p=0.186$ ).

Capture duration and poison latency for each prey type also varied according to predator stage (adult, juvenile). To estimate the role of relative prey weights and predator weights in the duration data, we made linear correlations between the index of weight (prey/scorpion) and durations. Non-significant regression values were obtained for capture duration of juvenile scorpions on crickets ( $r=0.134, p=0.711$ ), lycosids ( $r=0.100, p=0.850$ ) and amphinectids ( $r=0.102, p=0.727$ ), and for poison latency ( $r=0.028, p=0.937$ ;  $r=0.130, p=0.806$ ;  $r=0.314, p=0.274$ , respectively). Dysderids showed no variation in weight index.

**Discussion**

*Prey preference and capture tactic*

We consider *Tityus uruguayensis* to be mainly an araneophagic scorpion, based on its observed preferences for spiders compared with insects in both capture

	Adult scorpions			Juvenile scorpions		
	n	Capture attempts	Captures	n	Capture attempts	Captures
<b>Insects</b>						
Cockroaches	8	0	0	24	3	1
Mealworms	8	0	0	24	4	0
Crickets	8	7	2	24	18	10
<b>Spiders</b>						
Lycosids	8	7	4	24	20	6
Amphinectids	8	6	4	24	22	15
Dysderids	8	6	0	24	20	5

Table 5: Capture attempts and effective captures by adult and juvenile scorpions on three types of insect prey and three types of spider prey; n=number of observations.

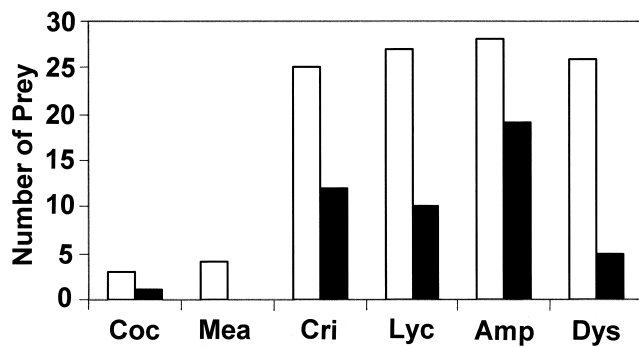


Fig. 2: Number of capture attempts and effective captures by adult and juvenile scorpions combined. Thirty-two trials were performed on each type of prey: cockroaches (Coc), mealworms (Mea), crickets (Cri), lycosids (Lyc), amphinectids (Amp) and dysderids (Dys). Open bars represent capture attempts and solid bars successful captures.

attempts and effective captures. The scorpions attacked all spider types (including the exotic and well-armed *Dysdera crocata*), whereas they ignored some insect prey such as mealworms and cockroaches. Mealworms and cockroaches are captured by a wide range of scorpion species belonging to the families Scorpionidae (Alexander, 1972), Vaejovidae (Bub & Bowerman, 1979; Cushing & Matherne, 1980) and Buthidae (Rein, 1993, 2003). However, crickets were frequently attacked and captured by *T. uruguayensis*, as happens with many other scorpions (Schultze, 1927; Bub & Bowerman, 1979; Cushing & Matherne, 1980; Casper, 1985). Changes in scorpion food preferences related to age or developmental stage were not suggested by the results, which showed similar preferences for juvenile and adult female scorpions. However, Casper (1985) found differences in the capture tactics of *Pandinus imperator* (C. L. Koch) (Scorpionidae) on crickets, according to its developmental stage: small juveniles always stung the prey but large juveniles only grasped it. Possibly, this last species is capable of capturing prey mechanically by using its strong pedipalps, and uses poison only when the prey is very large, unlike the predatory behaviour of *T. uruguayensis*.

As stated above, all prey types used in this work were selected because of their sympatry with the scorpion. *Metaltella simoni* is a cribellate web-builder, but this species is usually a good walker and frequently falls in pitfall traps, as reported by Costa *et al.* (1991), Costa

(1995), Costa & Simó (1999), Pérez-Miles *et al.* (1999) and Costa *et al.* (2003). Curiously, these authors also found adult females and juveniles in pitfall traps and not only adult males, as is usual for web-building spiders. These unusual locomotory characteristics make *M. simoni* a potential prey species for these scorpions.

Although *T. uruguayensis* seems to be a typical sit-and-wait predator, it showed an active but cautious approach to the prey (alert, orientation and grasp attempt units) after detecting it. Taking into account the poor visual capacity of scorpions, detection of prey is probably achieved by means of mechano- and/or chemoreception, because these senses are well-developed in these animals (see Brownell, 2001; Gaffin & Brownell, 2001). This species has very delicate chelae (Fig. 1), suggesting that its capture tactic would be that of an obligate stinger (Casper, 1985). Other scorpions, such as *Hadrurus* and *Paruroctonus* spp. (Vaejovidae), *Pandinus imperator* (Scorpionidae) and also buthid species belonging to *Buthus* and *Parabuthus*, have stronger chelae and the sting is selective, according to the size, resistance and type of prey (Cushing & Matherne, 1980; Casper, 1985; Rein, 1993, 2003). However, *T. uruguayensis* always stung the offered prey, independently of its type and level of resistance, and its poison was very effective. These scorpions always sting small prey or dead prey moved with forceps when they are fed in the laboratory (Toscano-Gadea, pers. obs.). The need for stinging possibly reflects a specialisation for capturing by poisoning. The slender chelae would be very sensitive, functioning for a quick grasp accompanied by a vigorous sting, but would not be used to mechanically subdue the prey. This is supported by the fact that the scorpions frequently released the prey after stinging. Delicate chelae would be useful to grasp the thin, long and numerous legs of spiders (and crickets); on the contrary, the cockroaches and mealworms we used are compact/round prey and it would be difficult for these scorpions to grasp these insects with their chelae. Additionally, *Tenebrio* larvae can wriggle as a defensive mechanism, but this tactic was rarely used because the scorpions usually did not attempt to capture them. The pedipalps of *T. uruguayensis* are also long and are used to hold dangerous prey as far as possible from the scorpion during the brief sting. In some cases, the scorpion continued to hold the stung prey, grasping it with only one extended pedipalp. However, the slender chelae

	n	Capture duration		Range	Mean	Poison latency		Range
		Mean	SD			SD	Range	
<b>Adult scorpions</b>								
Cricket	2	213.5	191.6	78–349	86.0	45.3	54–118	
Lycosids	4	150.3	158.8	26–383	36.6	16.3	23–60.2	
Amphinectids	4	299.4	403.8	4–870	47.5	23.4	23–73	
<b>Juvenile scorpions</b>								
Crickets	10	164.5	234.6	0–711	78.3	81.8	13–267	
Lycosids	6	150.3	195.9	0–484	68.5	95.0	14–253	
Amphinectids	15	140.8	222.6	0–628	42.2	35.5	0–144	
Dysderids	5	103.2	121.4	4–309	96.0*	29.0*	70–124*	

Table 6: Durations (s) of capture and poison latency of adult and juvenile scorpions preying on one type of insect and three types of spiders. Asterisks indicate data based on four cases, because one juvenile scorpion stung a dysderid but did not feed on it.

seem to be resistant to spider bites (three cases showed no observable damage).

#### *Antipredatory behaviour*

Escape was the main antipredatory behaviour shown by prey attacked by scorpions, but leg autotomy was also an effective mechanism of defence used by amphinectids and especially by lycosids, as stated also by Klawinski & Formanowicz (1994) and Punzo (1997). However, why did *T. uruguayensis* not capture dysderids? *Dysdera crocata* is a cosmopolitan spider that has invaded anthropic environments in Uruguay. Its conspicuous threatening display (Bristowe, 1941) appears to be an effective antipredatory behaviour; moreover, its mechanical and perhaps chemical defences (Pollard *et al.*, 1995) additionally make *D. crocata* a formidable opponent. Also, it is an "unknown" spider for this scorpion, which could not adapt to capture it. These characteristics possibly confused the scorpions, that recognised a spider and initially tried to capture it. However, some juvenile scorpions managed to overcome these defences and capture dysderids, and fed without any negative consequences. Therefore, it would seem that the putative chemical defences of *D. crocata* are not effective on *T. uruguayensis*. Summarising, *D. crocata* is recognised as a spider and attacked, but frequently the scorpions desist owing to its strong defences.

Crickets were attacked and constitute an exception for the araneophagic scorpion. Like spiders, crickets have long legs (mainly the hindlegs) that can be easily grasped, and the relatively soft skin allows the scorpion to sting easily. Coincidentally, crickets are usually attacked by buthids and other scorpions (Bub & Bowerman, 1979; Cushing & Matherne, 1980; Casper, 1985). Stung crickets were eaten starting at the head in almost all cases, as has been observed in other scorpions. Bub & Bowerman (1979) and Cushing & Matherne (1980), stated that this behaviour would help the scorpion by avoiding leg defences by poisoned crickets, because of the destruction of the central nervous system. However, Rein (1993, 2003) stressed that the cricket defence depends on ganglia located outside the brain and head destruction would not necessarily stop this kicking behaviour. Possibly, starting feeding at the head would simply permit this delicate scorpion to avoid as far as possible the hindlegs of the cricket, which constitute the cricket's main defensive weapon.

#### *Poisoning success*

The toxicity of *T. uruguayensis* venom seemed to be high for the arthropods used, as prey died quickly after being stung. Prey were often released after a single sting, which would support this assumption. We expected to find a correlation between prey/predator index of weight and the time spent after prey is stung until feeding. The absence of a correlation suggests that this poison is very effective for the selected sizes of prey, although the possibility that the scorpion estimates the prey size and

then adapts the poison dose, cannot be discarded. However, the high variation of latency values observed on all prey does not support this last hypothesis, it being more probable that this variation is related to the parts of the body where the prey were stung.

The closed dishes obviously favoured prey capture by scorpions. However, we do not make inferences here about real frequencies of capture but only comparative assumptions about capture attempts and effective captures on different types of prey under the same conditions, estimating their capacity to elicit and avoid capture. The scorpions had a standardised hunger rate owing to the similar previous period when they were deprived of food. We also simulated the situation of a sit-and-wait predator, first placing the scorpion into the experimental dishes and introducing prey after at least 24 h, thus allowing the predator to "acclimate" to the capture arena. Standardisation of prey-predator weights and hunger rate, and the situation of predator as resident (avoiding immediate previous manipulation) are conditions where we tried to improve on previous experiments on prey capture, as was pointed out by Rein (2003).

Two behaviours where the scorpions moved the stung prey (dragging and carrying) are possibly useful for eliciting responses from the prey and estimating the progress of poisoning. Carrying would also be useful for finding a protected site for eating the prey: this unit of behaviour (also called travelling with the prey) was reported by Bub & Bowerman (1979), Le Berre (1979), McCormick & Polis (1990) and Rein (2003). On the other hand, we could not find in the available literature any previous reports of dragging of the prey by scorpions.

Sagittal tail oscillations resemble manoeuvres preceding the stinging behaviour and perhaps denote intentional movements (Alcock, 1975) towards a poor but persistent stimulus (the subdued prey). Lateral tail oscillations, on the contrary, resemble advertisement movements, which are visually conspicuous and generate attention, conversely to what would be expected in a predatory context. They were frequent and had not previously been reported in relation to scorpion predation. The first author of this paper observed a similar display performed by young scorpions when bred together, sharing the same prey. However, the interpretation of this behaviour remains obscure.

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