








Pinching or stinging? Comparing prey capture among scorpions with contrasting morphologies

Luis Fernando García¹ , Juan Carlos Valenzuela-Rojas^{2*} , Julio César González-Gómez^{3,4} ,
Mariángeles Lacava⁵ , Arie van der Meijden^{3,6} 

¹Eastern Regional University Center (CURE), University of the Republic, Treinta y Tres, Uruguay.

²Semillero de Investigación INVUSCO, Grupo GIPB, Licenciatura en Ciencias Naturales y Educación Ambiental, Universidad Surcolombiana, Neiva, Huila, Colombia.

³Biology and Ecology of Arthropods (BEA) Research Group, Corporación Huitur, Neiva, Huila, Colombia and Merenberg Foundation, La Plata, Huila, Colombia.

⁴Graduate Program in Biological Sciences, School of Sciences, University of Tolima, Altos de Santa Helena, Ibagué, Tolima, Colombia.

⁵Rivera University Center (CENUR Noreste), University of the Republic (Udelar), Rivera, Uruguay.

⁶BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairão, Vairão, Portugal.

Keywords:

Bite force
Scorpions
Venom use
Predatory behavior

Abstract

Background: Scorpions can use their pincers and/or stingers to subdue and immobilize their prey. A scorpion can thus choose between strategies involving force or venom, or both, depending on what is required to subdue its prey. Scorpions vary greatly in the size and strength of their pincers, and in the efficacy of their venom. Whether this variability is driven by their defensive or prey incapacitation function is unknown. In this study, we test if scorpion species with different pincer morphologies and venom efficacies use these weapons differently during prey subjugation. To that end, we observed *Opisthacanthus elatus* and *Chactas* sp. with large pincers and *Centruroides edwardsii* and *Tityus* sp. with slender pincers.

Methods: The scorpion pinch force was measured, and behavioral experiments were performed with hard and soft prey (*Blaptica dubia* and *Acheta domesticus*). Stinger use, sting frequency and immobilization time were measured.

Results: We found that scorpions with large pincers such as *O. elatus* produce more force and use the stinger less, mostly subjugating prey by crushing them with the pincers. In *C. edwardsii* and *Tityus* sp. we found they use their slender and relatively weak pincers for holding the prey, but seem to predominantly use the stinger to subjugate them. On the other hand, *Chactas* sp. uses both strategies although it has a high pinch force.

Conclusions: Our results show that scorpion species with massive pincers and high pinch force as *O. elatus* use the stinger less for prey subjugation than scorpion species with slender pincers.

*Correspondence: juanbioquimico@gmail.com

<https://doi.org/10.1590/1678-9199-JVATITD-2021-0037>

Received: 06 April 2021; Accepted: 20 August 2021; Published online: 01 April 2022



Background

Morphology, through its influence on performance, can be linked to some key ecological functions including mating and feeding or defensive behavior [1]. The role of morphology in feeding has been widely explored in vertebrates. For example, some studies have shown that mammal and fish feeding ecology has a stronger evolutionary influence on functional morphology [2,3]. There are a small but increasing number of functional studies exploring the relationship between morphology and feeding ecology in invertebrates, mainly in arachnids and insects [4–8]. A few studies have shown that some parameters, including shape and force, play a key role in prey capture in some predators. For example, crabs with larger claws are able to feed upon larger and harder shells, suggesting a specialization in this prey type [9].

Prey body hardness is considered to be an important defensive mechanism and it is present in a wide variety of animals with hard defensive shells such as armadillos, turtles, alligator and fish [10]. In arthropods, this defensive mechanism is present in numerous taxa, such as beetles, isopods and other arthropods [11–14]. For predators that need to grasp or crush their prey with mandibles, prey hardness represents a challenging parameter. For example, shell hardness might limit the capture ability in some fish and crabs [10,15]. Similarly, some spiders that crush their prey are less efficient than spiders that attack soft spots when capturing hard-bodied prey [16]. Prey morphology is known to determine predatory strategy in several groups including scorpions [17]. Since scorpions use both strategies, piercing soft body parts using the stinger and crushing the body with the pincers (chela), we consider them a good model to evaluate the effect of prey hardness on feeding strategy. We expect these generalist predators may employ alternative prey capture strategies depending on prey morphology.

Scorpions are a successful group of terrestrial arthropods, present in almost all known terrestrial habitats [18]. Although the high success of this group has been attributed to several traits, morphology plays a key role, particularly their chelae and metasoma that are linked to defense and predation [19]. Among the most characteristic structures in scorpions are the chelae and stinger (telson), which are considered the main weapons and affect several ecological functions in scorpions, including prey capture, defense, sensing and mating [20]. In scorpions, the chelae are pincer-like structures, which vary in strength. The strength correlates with morphological parameters of the chela, particularly the width and height of muscular part of the manus [4]. Pinch force is higher in scorpions with robust chela when compared to species with slender structures. Scorpion morphology is highly variable: some species have robust, powerful chelae, while some others have slender chelae [20]. There are also large differences in the morphology and performance of the stinger and its venom, and the shape and size of the tail-like metasoma that carries the stinger. Scorpions with massive chelae use this structure as their main defensive

strategy, whereas scorpions with slender chelae use the stinger more frequently, suggesting a possible tradeoff between these structures [21].

Feeding ecology has been studied for some scorpion species. However, most of these studies have focused on field observations [22–24]. Most studies regarding prey capture have evaluated the role of sting use in prey capture. In some species, sting use can change ontogenetically, with juveniles stinging their prey more frequently than adult individuals [25]. Sting use may also depend on prey activity and resistance, and some species use it only against large, potentially dangerous or highly mobile prey. González-Gomez et al. [6] have shown that scorpions with slender chelae are more toxic for insect prey such as *Tenebrio molitor* Linnaeus, 1758 larvae, which might explain why these scorpions use stinger more frequently in prey capture. However, it is unknown if this pattern is present in other scorpion species and whether it varies depending on prey type. Despite the frequent use of venom in prey capture, scorpions are able to subdue their prey using only the chelae [20]. However, Evans et al. [26] extensively discuss how the mobility and size of prey, presence of predators, and environmental factors such as temperature can affect the use and toxicity of scorpion venom.

The aim of this paper is to evaluate the role of chela force on the prey handling behavior in different scorpion species with contrasting chela morphologies. These range from species with slender and weak chelae to species with robust and very strong chelae. In addition, we evaluate if there is a relationship between chela force and stinger use, and if these traits are dependent on prey type. Since scorpions with stronger chelae tend to use them more [5], we hypothesized that scorpions with stronger chelae would have a lower sting use compared to scorpions with slender chelae. If there exists a tradeoff between sting use and chela morphology, we expect a similar predatory efficiency between species with contrasting morphologies against soft prey, but a higher efficiency of species with strong chelae against hard prey. This as species with robust chelae can, in addition to stinging, use crushing as a means to incapacitate the prey.

Methods

Species selection

We selected four scorpion species with contrasting morphologies. As a species with robust chelae, we selected *Opisthacanthus elatus* (Hormuridae) Gervais, 1844 from San José-Santander Valley (06° 26'53.65"N 73° 8'20.32"W), this species is often found under rocks where it makes a shallow burrow. We also selected *Chactas* sp. (Chactidae) from Termales los Ángeles, Rivera-Huila (02° 45' 06.6"N 75° 14'17.0" W), as in this species the females have robust chelae, and the males have slender chelae. Individuals of this species were observed at the entrance of their burrows during the night, especially females. As model species with slender chelae, we chose *Tityus* sp. (Buthidae)

collected in a forest in the Universidad Surcolombiana campus in Neiva-Huila (2° 56'40.417"N 75° 18'6.952" W) and *Centruroides edwardsii* (Buthidae) Gervais, 1843 in the Desierto de la Tatacoa, Villavieja-Huila (03° 5'31.61"N 75° 8'25.08" W). We collected a total of 76 specimens (Table 1). Both buthid species were observed actively looking for prey during the night. Although information about the trophic ecology of these species is scarce, preliminary observations suggests all selected scorpion species possess a generalist diet.

Once collected, all individuals were housed individually in plastic boxes (12x9x6cm). Water was provided *ad libitum* to each scorpion species using wet cotton. Photoperiod (12 light:12 dark), temperature (26°C) and humidity (70%) were held constant during the study. Experiments were done at the BEA laboratory, and voucher specimens were deposited in the Colección Zoológica de la Universidad del Tolima (CZUT).

Collected individuals were randomly assigned to bite force measurement or behavioral experiments using the R software [27].

Table 1. Morphological characters of males and females of the four species of studied scorpions.

Species	Sex	Morphological characters – All sizes are in mm (mean ± SE)			
		Prosoma		Chela	
		Length	Width	Length	Width
<i>Centruroides edwardsii</i>	Female (n = 9)	8.3 ± 0.21	7 ± 0.23	13.4 ± 0.51	3.6 ± 0.2
	Male (n = 11)	8.8 ± 0.26	6.9 ± 0.23	14.9 ± 0.52	4.1 ± 0.15
<i>Chactas</i> sp.	Female (n = 8)	6.4 ± 0.16	5.4 ± 0.11	11 ± 0.2	3.7 ± 0.2
	Male (n = 8)	6.5 ± 0.14	5.4 ± 0.12	13.9 ± 0.49	3 ± 0.15
<i>Opisthacanthus elatus</i>	Female (n = 12)	11.7 ± 0.27	11.3 ± 0.37	22.6 ± 0.58	9.2 ± 0.34
	Male (n = 8)	11.7 ± 0.46	10.9 ± 0.54	21.4 ± 1.33	8.2 ± 0.45
<i>Tityus</i> sp.	Female (n = 12)	7.1 ± 0.23	6 ± 0.18	12.6 ± 0.47	2.7 ± 0.08
	Male (n = 8)	6.8 ± 0.27	5.8 ± 0.23	13.6 ± 0.58	3.5 ± 0.11

Bite force measurement

We randomly selected males and females of each scorpion species, namely:

- *O. elatus* –n = 20; 8 males and 12 females;
- *Chactas* sp. –n = 20; 7 males and 13 females;
- *Tityus* sp. –n = 23; 8 males and 15 females;
- *C. edwardsii* –n = 19; 11 males and 8 females.

We measured the bite force using a Kistler low-force sensor, type 9203, connected to a one-channel hand-held charge amplifier, type 5995A (see Additional file 1). Force was transmitted to the sensor by custom-built plates [4,6]. To measure the bite force, scorpions were immobilized except for their chelae which were placed on the sensor plates and the scorpions were stimulated to bite them. Bite force of each pedipalp was measured once per day for five days consecutively. We use only the maximum bite forces of each scorpion for the analysis. The measurements were made at a controlled temperature (25±1°C) following the methods described by González-Gómez et al. [6].

Once bite force was measured, it was compared among the different scorpion species using a linear model with the scorpion species and sex as explanatory variables, while log-transformed force was used as response variable.

Behavioral experiments

We compared the sting use and feeding efficiency of the selected scorpion species against prey with different morphologies (Figure 1). As a soft prey, we used crickets (*Acheta domesticus* Linnaeus, 1758) and as a hard prey we used cockroaches (*Blaptica dubia* Serville, 1839) (Table 2), as some species of cockroaches are known to have a tough exoskeleton which is able to withstand forces several times higher than their own body weight [28]. To standardize hunger levels, scorpions were fed to satiation two weeks before starting the experiments with *T. molitor* larvae [17]. All experiments were carried out in plastic boxes (12x9x6cm) that were sterilized with 70% alcohol and water between each trial to remove any olfactory remains of the previous experiment. All videos were recorded with a Nikon D7000 camera. We used red LED lights to illuminate the experiments, because these do not affect the scorpions' behavior [29].

Table 2. Length of the prey. All measurements are in mm. Length from head to end of abdomen (mean ± SE).

Species of prey	Prey length
<i>Acheta domesticus</i> (n = 76)	14.6 ± 0.3
<i>Blaptica dubia</i> (n = 76)	17.2 ± 0.4

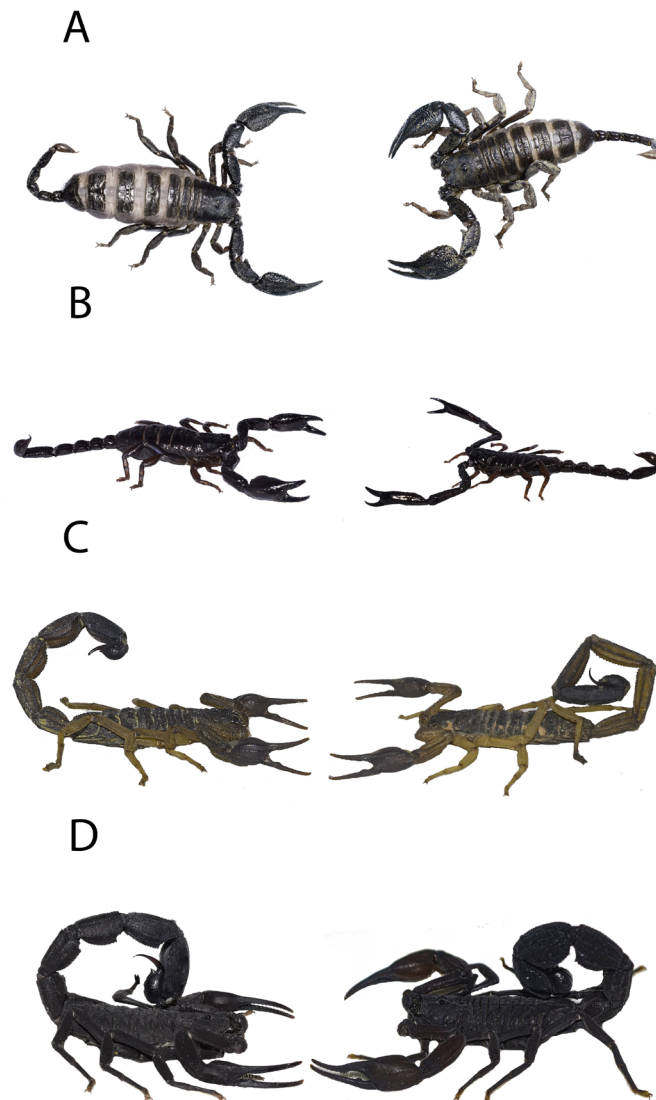


Figure 1. Habitus of the scorpions used on this study. On the left females are presented and on the right, males. **(A)** *Opisthacanthus elatus*, **(B)** *Chactas* sp., **(C)** *Centruroides edwardsii*, and **(D)** *Tityus* sp.

Each prey type was presented randomly to each scorpion, using a complete random block design [30]. In each experiment, we placed the prey at the opposite end of the scorpion's box (about 6cm away) and recorded the total immobilization time, which was considered as the time interval from the first contact between the scorpion and the prey until it stopped moving. We also recorded whether, and how often, the stinger pierced the prey to paralyze it.

Given that relative size might influence prey capture in scorpions, we evaluated the effect of prey:predator size ratio (Additional file 2) on sting use and immobilization time. For scorpions and their prey morphometric data were obtained by photographing individuals with a size standard using a Nikon D7000 digital camera and measuring them with the program ImageJ [31]. We estimated the prey:scorpion size ratio for selected traits, namely the scorpion's prosoma length and width and chelae length and width (Table 1). Given that size ratio for the morphological traits we selected presented a strong collinearity,

we created a new variable (hereafter name Relative Size), by applying a principal component analysis to the prey:scorpion size ratio for the chosen morphological variables and then extracting the first component which explained 93% of the observed variability, as suggested by Zuur et al [32].

Sting use

We compared sting use on crickets and cockroaches among the different scorpion species. Data were analyzed using a generalized estimating equation with a binomial distribution (GEE-b) [33], given that same individuals were used more than once. Scorpion species, prey type and relative size were used as explanatory variables. Scorpion individual was considered as random variable. In this analysis, we included Stinger Use as a response variable. When not stung, we observed if the scorpion crushed the prey. We defined as crush, when the scorpion repeatedly pressed the prey using pedipalps.

Immobilization time

To test if immobilization time was different between species, we used log-transformed Immobilization Time as the response variable and we used the Stinger Use, Prey Type and Relative Size as explanatory variables. Relative Size was included as it influences immobilization time in other venomous predators such as spiders [34]. We also looked for potential interactions between Scorpion Species and Stinger Use as well as Scorpion Species and Relative Size. All analyses were made using a GEE with a Gaussian distribution, give the data observed distribution.

Results

Chelae bite force

We found a marked and significant difference on pinch force between the evaluated species ($F_{(7,68)} = 130$, $p < 0.01$). Post-hoc comparisons showed the highest force for *O. elatus*, followed by females and males of *Chactas* sp. respectively. Still lower force values were recorded for both sexes of *C. edwardsii*, and the weakest pinch forces were recorded in *Tityus* sp. (Additional file 1) mean forces and confidence intervals are illustrated in Figure 2.

Sting use

We found a significant interaction between scorpion species and prey type ($\chi^2_3 = 4.78 \times 10^{21}$, $p < 0.01$). Some species like *O.*

elatus used their sting only against cockroaches while crickets were never stung and their body collapsed several times when crushed by the scorpion's pedipalps (Figure 3, Additional files 3 and 4). In contrast to the other species, *Chactas* sp. stung both prey, but crickets were always stung (Additional files 5 and 6), while cockroaches were stung less frequently than crickets but in similar proportions to the other scorpion species (Additional file 6). Both buthid species always stung both offered prey types, while holding them with their pedipalps (Additional files 7-10). Overall, we did not find a significant effect of relative size ($\chi^2_1 = 2.00$, $p = 0.12$) or sex ($\chi^2_1 = 1.00$, $p = 0.72$) on the stinger use. All videos are also available in a playlist (<https://bit.ly/3HOvWRC>).

Immobilization time

Overall, we found that Immobilization Time significantly increased with the Relative Size ($\chi^2_1 = 4.4$, $p = 0.035$), and we also found significant differences with Scorpion Species ($\chi^2_3 = 34.0$, $p < 0.01$) and Prey Type ($\chi^2_1 = 35.4$, $p < 0.01$). Post-hoc comparisons showed that immobilization time for *C. edwardsii* was significantly longer than the other species (Figure 4A). When we compared both prey types, we found that the immobilization time for cockroaches was significantly longer when compared to crickets (Figure 4B). Surprisingly, stinger use did not affect the immobilization time ($\chi^2_1 = 0.70$, $p = 0.40$).

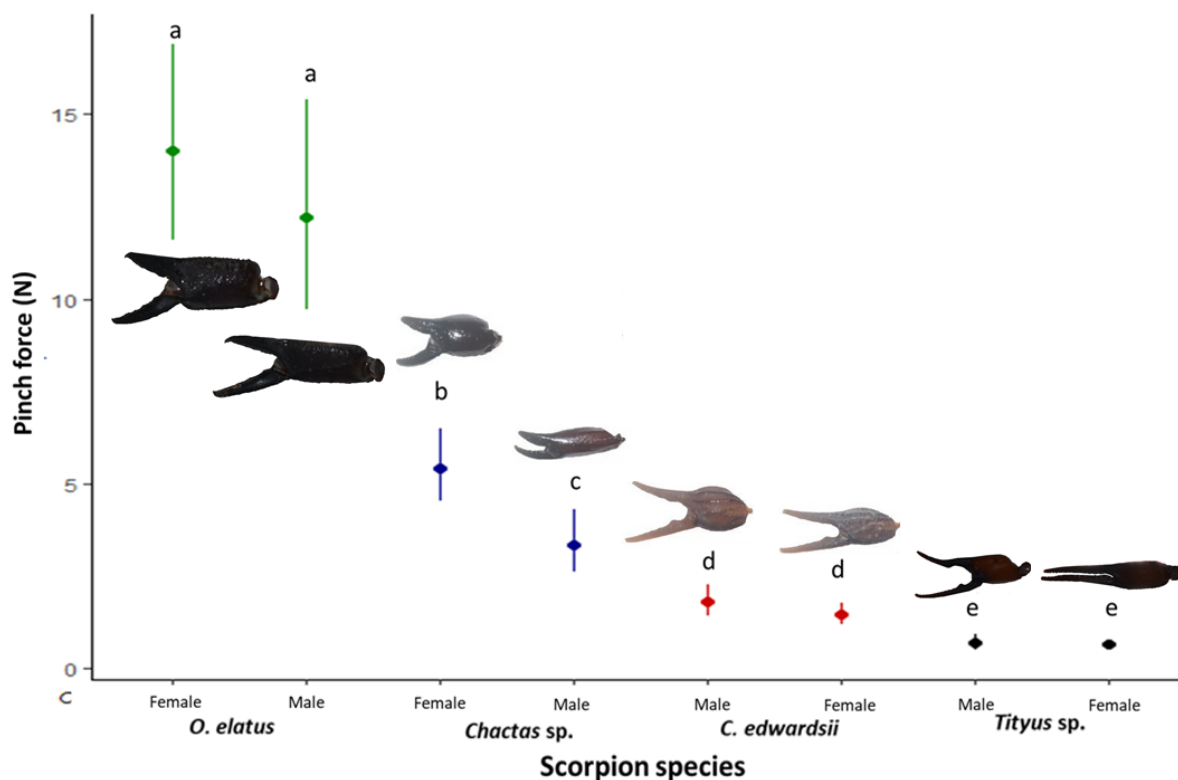


Figure 2. Pinch forces of different species and genders of scorpions. Points are means whereas lines are confidence intervals. Letters indicate significant differences. Parameters were estimated using a linear model. The size of the chelae are not to scale.

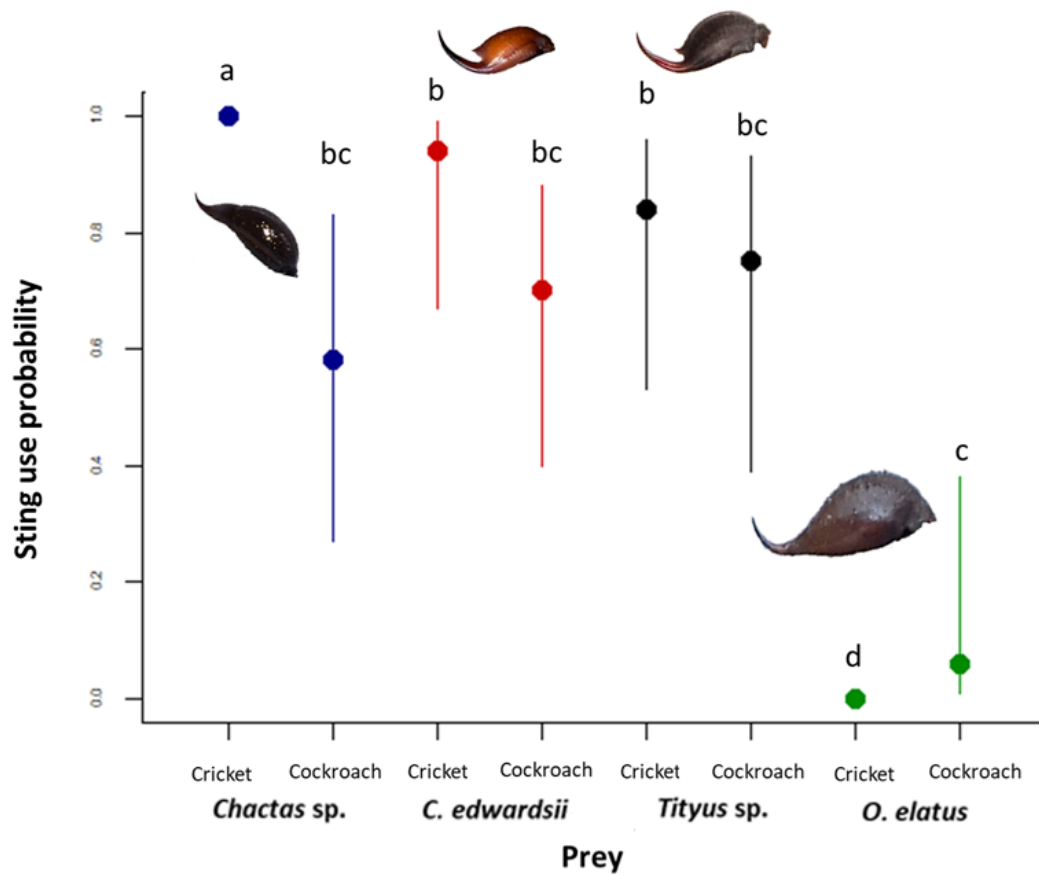


Figure 3. Sting use probability of the different species of scorpions. Points are means and lines are confidence intervals. Letters indicate significant differences. Parameters were estimated using a Generalized Estimated Equation with a binomial distribution. The size of the stingers are not to scale.

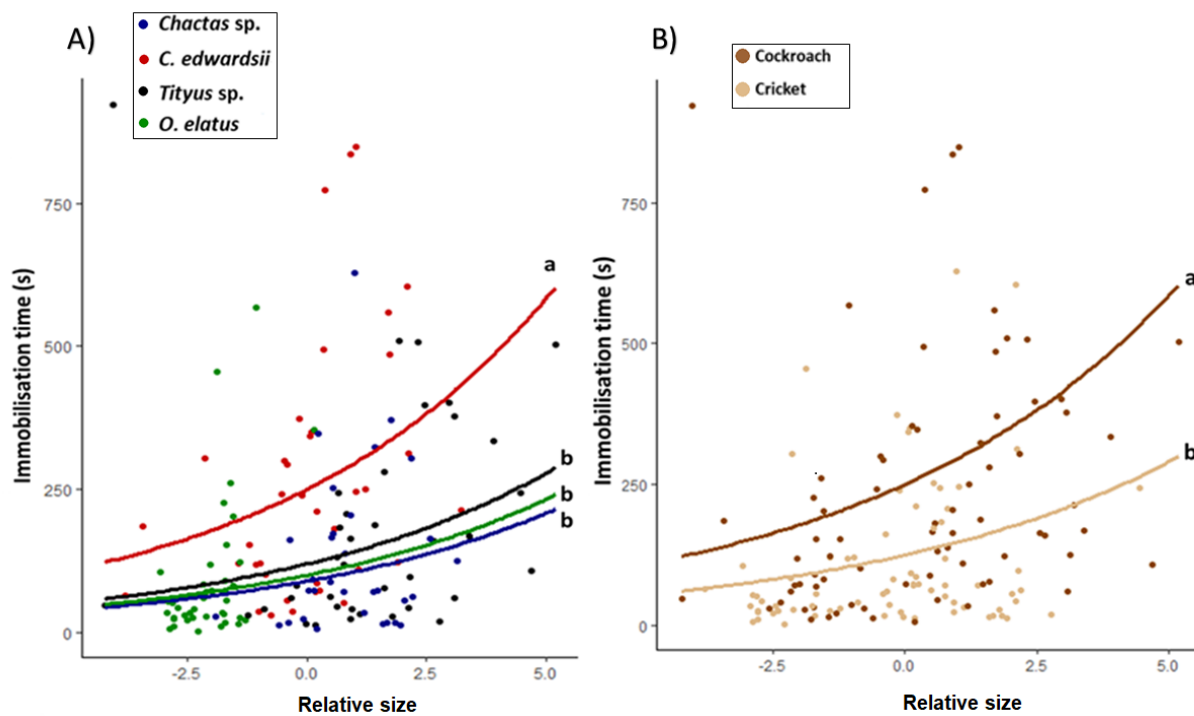


Figure 4. Immobilization time of the different species by: (A) scorpion species and (B) prey species. Letters indicate significant differences. Parameters were estimated using a generalized estimated equation with Gaussian distribution.

Discussion

Venom is considered a metabolically expensive product and its usage must be regulated by the scorpions. Several hypotheses have been proposed to explain the optimal use and toxicity in scorpions. According to Evans et al. [26], the use of large pedipalps is often accompanied with small stingers, while the opposite trend is observed in scorpions with slender pedipalps. As a consequence, venom use should be optimized depending on scorpion morphology, being more frequent in scorpions with a low pinch force [5].

When we compared the pinch force in all evaluated species, *O. elatus* has the highest pinch force of all evaluated species, followed by *Chactas* sp., where females were stronger males. However, both sexes of *Chactas* sp. had a higher pinch force than both the evaluated buthid species. In *Tityus* sp. we recorded a lower pinch force than in *C. edwardsii*, probably because of the more slender chelae found in the former species. In the particular case of *Chactas* sp., males have slenderer chelae than females, which might explain the higher pinch force of the latter. This agrees with previous studies which suggest that scorpions with robust chelae are stronger than species with slender chelae [4,5,35]. Since we did not correct for overall body size, the between-species comparisons are no indication for relative pinch performance.

We found a different sting use between the studied species. For example, *O. elatus* used their sting occasionally against cockroaches, while crickets were never stung. We hypothesize that pedipalp pinch force in this species is enough to overcome soft and highly mobile prey like crickets, and to overcome most harder prey like cockroaches. This species therefore uses a similar strategy to some predators with massive claws, like some crabs which crush their prey [9]. During prey capture we observed that some structures like head and thorax were repeatedly crushed by *O. elatus*, probably to incapacitate the prey, or to facilitate prey ingestion, similarly to other predators like spiders [36,37]. Cockroaches were more frequently stung than crickets by *O. elatus*, probably as their tough exoskeleton did not collapse under repeated pinches. In both buthid (*Tityus* sp. and *C. edwardsii*) scorpion species, the stinger was used for both prey types, probably because the weaker chelae were not even able to crush soft-bodied prey such as crickets. This may also explain why previous studies found species with slender chelae to more frequently use their stinger against potential predators [21,38]. However, this hypothesis of insufficient force being augmented with stinging needs to be further tested, as there may also be other relevant factors, such as behavioral preferences or the prey's defensive behavior.

Immobilization time was affected by prey: predator size ratio. This is an expected result given that larger prey are usually harder to subdue than smaller ones [39]. Similarly, large prey might require more venom to be subdued because of their size and mass. This may be why, even when stung, very large prey were hard to paralyze. However, this would suggest that scorpions do not release enough venom on the first sting when estimating prey size, but instead measure venom by applying

multiple consecutive stings until the prey stops moving [40]. Such behavior may be a function of the size of the prey, as it has been demonstrated in *Hadrurus spadix* Stahnke, 1940, which also shows a positive relationship between sting use and prey size [40]. However, prey size and prey activity may both influence venom administration [41]. Although we expected scorpions with a similar morphology to have similar immobilization times, this was not the case, since all scorpions had similar immobilization times against offered prey except for *C. edwardsii*. Interestingly, scorpions with contrasting morphologies such as *Tityus* sp. and *O. elatus* displayed similar performance against offered prey, independent of whether these were hard or soft-bodied. This suggests that by using venom and/or chelae, incapacitation performance was similar between these species. A similar trend has been observed in some snakes where constriction might be equally or more effective than the use of toxins when subduing prey, underlining the importance of mechanical strategies during prey incapacitation [42,43].

Although not significantly different, we observed that immobilization time was shorter for *Chactas* sp. than for the other species, suggesting that it was slightly more efficient than both aforementioned species. This might be due to *Chactas* sp. using both strong chelae and stinging during prey capture. However, since *Chactas* sp. was also the smallest species we studied, this difference may also be a result of scaling effects. Although their morphologies and prey capture strategies are similar, *C. edwardsii* and *Tityus* sp. were not similarly effective in prey incapacitation, and the former species was less efficient than the latter during prey capture. We hypothesize that the differences recorded in predatory efficiency between *C. edwardsii* and *Tityus* sp. might be explained by a difference in the toxicity of the venom. Although a high insecticidal toxicity has been reported for several *Tityus* species [44,45], the effect of *C. edwardsii* venoms against potential insect prey is reported to be variable, with crickets being more susceptible, while the cockroaches and the mealworms are more resistant [46].

When comparing capture efficiency against the offered prey species, we observed that cockroaches were harder to immobilize than crickets, which may be due to the former having a tougher body with a more difficult to penetrate exoskeleton. Cockroaches also have been reported to be more resistant against some toxins like those of some spider species [47] and other scorpions like *C. edwardsii*. Crickets have been reported to be more susceptible to scorpion venom [46], and are also soft-bodied, making them more susceptible to being crushed.

Although using a limited number of prey and predator species, this is to our knowledge the first study to compare the role of chelae and stinging in prey capture in scorpion species with contrasting morphologies.

Conclusion

We found that scorpions with robust chelae and slender metasoma such as *O. elatus*, not only have a high pinch force, but also a

reduced sting use, suggesting that prey crushing is the main prey incapacitation strategy for this species, even when facing hard-bodied prey. The two buthid (*Tityus* sp. and *C. edwardsii*) species used the stinger more frequently to incapacitate their prey. Interestingly, we identified the scorpion *Chactas* sp. as using a mixed strategy, with high pinch force and sting use that allowed them to overcome quickly both prey types offered (Additional files 5 and 6). In the case of buthid scorpions, although both species used the same strategy (forces and sting use), we found differences in immobilization time, which might be explained by a difference in the toxicity of the venom to insects. Although our study shows a trade-off between pinch force and sting use in some species and mixed strategy in others, further studies should explore if the trends observed for the species on this study are applicable for other scorpions with similar morphologies, and could include other effects of prey morphology and behavior such as dangerous or highly active prey.

Acknowledgments

We express our gratitude to Fanny C. Ariza, Julio C. Prieto and Denier Y. Ramírez for their support in the development of this project. Also, to Daniel Ramírez and Hilda R. Mosquera, from the GEBIUT Research Group of the University of Tolima, for the equipment and location. Finally, to Roberto Builes for his donation of prey for the experiments. Alejandra Arroyave kindly provided the *Opisthacanthus elatus* images. Stano Pekár assisted us with a part of statistical analyses.

Availability of data and materials

The dataset generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Funding

LFG was funded by Agencia Nacional de Investigación e Innovación (ANII) and full time program (DT) by the Comisión Sectorial de Investigación Científica (CSIC), Universidad de la República. AvdM was financed through FCT – Fundação para a Ciência e a Tecnologia, I.P. under contract number DL57/2016/CP1440/CT0009.

Competing interests

The authors declare that they have no competing interest.

Authors' contributions

LFG, JCV-R, JCG-G and AVDM, conceived this research and designed experiments. LFG, JCV-R and MLM wrote the main manuscript. JCV-R, and JCG-G carried out all behavioral experiments. MLM and LFG analyzed all data. All authors revised and approved the final manuscript.

Ethics approval

All animal care was in accordance with appropriate ethical guidelines and animal collection was approved by Resolución no. 1462 (3 Dec. 2014), Autoridad Nacional de Licencias Ambientales (ANLA).

Consent for publication

Not applicable.

Supplementary material

The following online material is available for this article:

Additional file 1. Force measurements (in Newtons) in different species of scorpions.

Additional file 2. Prey:predator size ratio (mean \pm SD) for the different morphological measurements.

Additional file 3. Video showing *Opisthacanthus elatus* feeding on a cockroach (*Blaptica dubia*).

Additional file 4. Video showing *Opisthacanthus elatus* feeding on a cricket (*Acheta domesticus*).

Additional file 5. Video showing *Chactas* sp. feeding on a cockroach (*Blaptica dubia*).

Additional file 6. Video showing *Chactas* sp. feeding on a cricket (*Acheta domesticus*).

Additional file 7. Video showing *Tityus* sp. feeding on a cockroach (*Blaptica dubia*).

Additional file 8. Video showing *Tityus* sp. feeding on a cricket (*Acheta domesticus*).

Additional file 9. Video showing *Centruroides edwardsii* feeding on a cricket (*Acheta domesticus*).

Additional file 10. Video showing *Centruroides edwardsii* feeding on a cockroach (*Blaptica dubia*).

References

1. Taborsky M. From Ethology to Behavioral Biology. In: Chun C. J., editor. Encyclopedia of Animal Behavior. 2nd edition. Elsevier. p. 99–102. 2019.
2. Grossnickle DM. Feeding ecology has a stronger evolutionary influence on functional morphology than on body mass in mammals. *Evolution*. 2020 Mar;74(3):610–28.
3. Wainwright PC. Morphology and Ecology: Functional Basis of Feeding Constraints in Caribbean Labrid Fishes. *Ecology*. 1988;69(3):635–45.
4. van der Meijden A, Herrel A, Summers A. Comparison of chela size and pincer force in scorpions; getting a first grip. *J Zool*. 2010;280:319–25.
5. van der Meijden A, Kleinteich T, Coelho P. Packing a pinch: functional implications of chela shapes in scorpions using finite element analysis. *J Anat*. 2012 May;220(5):423–34.
6. González-Gómez JC, Valenzuela-Rojas JC, García LF, Franco Pérez LM, Guevara G, Buitrago S, Cubillos A, van der Meijden AV. Sexual dimorphism in the biomechanical and toxicological performance in prey incapacitation of two morphologically distinct scorpion species (*Chactas* sp. and *Centruroides* sp.). *Biol J Linn Soc. Oxford Academic*; 2020 Nov;129:190–8.

7. Rodriguez G, Fikáček M, Minoshima YN, Archangelsky M, Torres PLM. Going underwater: multiple origins and functional morphology of piercing-sucking feeding and tracheal system adaptations in water scavenger beetle larvae (Coleoptera: Hydrophiloidea). *Zool J Linnean Soc*. 2020 Sep;193(1):1-30.
8. Kundanati L, Chahare NR, Jaddivada S, Karkisaval AG, Sridhar R, Pugno NM, Gundiah N. Cutting mechanics of wood by beetle larval mandibles. *J Mech Behav Biomed Mater*. 2020 Dec;112:104027.
9. Yamada SB, Boulding EG. Claw morphology, prey size selection and foraging efficiency in generalist and specialist shell-breaking crabs. *J Exp Mar Biol Ecol*. 1998 Feb;220(2):191-211.
10. Yang W, Chen IH, Mckittrick J, Meyers MA. Flexible dermal armor in nature. *JOM*. 2012;64:475-85.
11. Witz BW. Antipredator mechanisms in arthropods: a twenty year literature survey. *Florida Entomol*. 1990 Mar;73(1):71-99.
12. Noh MY, Muthukrishnan S, Kramer KJ, Arakane Y. Cuticle formation and pigmentation in beetles. *Curr Opin Insect Sci*. 2016 Oct;17:1-9.
13. Vittori M, Vodnik K, Blejec A. Changes in cuticle structure during growth in two terrestrial isopods (Crustacea: Isopoda: Oniscidea). *Nauplius*. 2020;28:2358-936.
14. Sugiura S. Predators as drivers of insect defenses. *Entomol Sci*. 2020;23(3):316-37.
15. Woodbury PB. The geometry of predator avoidance by the blue crab, *Callinectes sapidus* Rathbun. *Anim Behav*. 1986 Feb;34:28-37.
16. Segovia JMG, Del-Claro K, Willemart RH. Delicate fangs, smart killing: the predation strategy of the recluse spider. *Anim Behav*. 2015;101:169-77.
17. Simone Y, Garcia LF, Lacava M, van der Meijden A, Viera C. Predatory versatility in females of the scorpion *Bothriurus bonariensis* (Scorpiones: Bothriuridae): overcoming prey with different defensive mechanisms. *J Insect Behav*. 2018;31:402-15.
18. Polis GA. *The Biology of Scorpions*. Stanford University Press; 1990.
19. Lourenço WR. The coevolution between telson morphology and venom glands in scorpions (Arachnida). *J Venom Anim Toxins incl Trop Dis*. 2020;26. <https://doi.org/10.1590/1678-9199-JVATITD-2020-0128>.
20. Sridhara S, Chakravarthy AK, Kalarani V, Reddy DC. Diversity and Ecology of Scorpions: Evolutionary Success Through Venom. In: Chakravarthy AK, Sridhara S, editors. *Arthropod Diversity and Conservation in the Tropics and Sub-tropics*. Singapore: Springer. p. 57-80. 2016.
21. van der Meijden A, Coelho PL, Sousa P, Herrel A. Choose your weapon: defensive behavior is associated with morphology and performance in scorpions. *PLoS One*. 2013 Nov 13;8(11):e78955.
22. Polis GA, Sissom DW, McCormick SJ. Predators of scorpions: field data and a review. *J Arid Environ*. 1981;4(4):309-26.
23. Polis GA, Myers CA, Holt RD. The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annu Rev Ecol Evol Syst*. 1989;20:297-330.
24. Valdez JW. Arthropods as vertebrate predators: a review of global patterns. *Global Ecol Biogeogr*. 2020 Feb:1-13.
25. Cushing BS, Matherne A. Stinger utilization and predation in the scorpion *Paruroctonus boreus*. *Great Basin Nat*. 1980;40(2):193-5.
26. Evans ERJ, Northfield TD, Daly NL, Wilson DT. Venom costs and optimization in scorpions. *Front Ecol Evol*. 2019;7:196.
27. R Development Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing. The R Project for Statistical Computing Getting Started. 2018. Available from: <http://www.R-project.org>.
28. Jayaram K, Full RJ. Cockroaches traverse crevices, crawl rapidly in confined spaces, and inspire a soft, legged robot. *PNAS*. 2016 Feb 23;113(8):E950-7.
29. Machan L. Spectral sensitivity of scorpion eyes and the possible role of shielding pigment effect. *J Exp Biol*. 1968;49(1):95-105.
30. Pekár S, García LF, Viera C. Trophic Niches and Trophic Adaptations of Prey-Specialized Spiders from the Neotropics: A Guide. In: Viera C, Gonzaga MO, editors. *Behaviour and Ecology of Spiders: Contributions from the Neotropical Region*. Cham: Springer International Publishing. p. 247-74. 2017.
31. Schneider CA, Rasband WS, Eliceiri KW. NIH Image to ImageJ: 25 years of image analysis. *Nat Methods*. 2012 Jul;9(7):671-5.
32. Zuur AF, Ieno EN, Elphick CS. A protocol for data exploration to avoid common statistical problems. *Methods Ecol Evol*. 2010;1(1):3-14.
33. Yan J, Fine J. Estimating equations for association structures. *Stat Med*. 2004 Mar 30;23(6):859-74.
34. Pekár S, Brabec M. *Modern Analysis of Biological Data: Generalized Linear Models in R*. Masarykova univerzita; 2016.
35. Simone Y, van der Meijden A. Fast and fine versus strong and stout: a trade-off between chela closing force and speed across nine scorpion species. *Biol J Linn Soc*. 2018 Jan;123(1):208-17.
36. García LF, Franco V, Robledo-Ospina LE, Viera C, Lacava M, Willemart RH. The predation strategy of the Recluse Spider *Loxosceles rufipes* (Lucas, 1834) against four prey species. *J Insect Behav*. 2016;29:515-26.
37. García LF, Rave C, Arcila K, García C, Robledo-Ospina LE, Willemart R. Do predators react differently to dangerous and larger prey? The case of a mygalomorph generalist spider preying upon insects. *Zoology (Jena)*. 2020 Feb;144:125863.
38. Carlson BE, McGinley S, Rowe MP. Meek males and fighting females: sexually-dimorphic antipredator behavior and locomotor performance is explained by morphology in bark scorpions (*Centruroides vittatus*). *PLoS One*. 2014 May 28;9(5):e97648.
39. Mukherjee S, Heithaus MR. Dangerous prey and daring predators: a review. *Biol Rev Camb Philos Soc*. 2013 Aug;88(3):550-63.
40. Edmunds MC, Sibly RM. Optimal sting use in the feeding behavior of the scorpion *Hadrurus spadix*. *J Arachnol. Am Arachnol Soc*. 2010 Apr 1;38(1):123-5.
41. Wigger E, Kuhn-Nentwig L, Nentwig W. The venom optimisation hypothesis: a spider injects large venom quantities only into difficult prey types. *Toxicon*. 2002 Jun;40(6):749-52.
42. Moon BR, Penning DA, Segall M, Herrel A. Feeding in Snakes: Form, Function, and Evolution of the Feeding System. In: Bels V, Whishaw IQ, editors. *Feeding in Vertebrates: Evolution, Morphology, Behavior, Biomechanics*. Cham: Springer International Publishing. p. 527-74. 2019.
43. Shine R, Schwaner T. Prey constriction by venomous snakes: a review, and new data on Australian species. *Copeia*. 1985 Dec 10;1985(4):1067-71.
44. Oliveira UC de, Nishiyama Jr MY, Santos MBV dos, Santos-da-Silva A de P, Chalkidias H de M, Souza-Imberg A, Candido DM, Yamanouye N, Dorce VAC, Junqueira-de-Azevedo ILM. Proteomic endorsed transcriptomic profiles of venom glands from *Tityus obscurus* and *T. serrulatus* scorpions. *PLoS One*. 2018 Mar 21;13(3):e0193739.
45. Cologna CT, Peigneur S, Rustiguel JK, Nonato MC, Tytgat J, Arantes EC. Investigation of the relationship between the structure and function of Ts2, a neurotoxin from *Tityus serrulatus* venom. *FEBS J*. 2012 Apr;279(8):1495-504.
46. Díaz C, Rivera J, Lomonte B, Bonilla F, Diego-García E, Camacho E, Tytgat J, Sasa M. Venom characterization of the bark scorpion *Centruroides edwardsii* (Gervais 1843): Composition, biochemical activities and *in vivo* toxicity for potential prey. *Toxicon*. 2019 Dec 5;171:7-19.
47. Friedel T, Nentwig W. Immobilizing and lethal effects of spider venoms on the cockroach and the common mealbeetle. *Toxicon*. 1989;27(3):305-16.