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SHORT COMMUNICATION

Optimal sting use in the feeding behavior of the scorpion *Hadrurus spadix*

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Abstract. Since venom is costly to produce and stinging is not obligatory in prey capture for scorpions, the need to optimize use of resources suggests that venom should be reserved for prey that cannot otherwise be overpowered, (i.e., larger and/or more active prey). In accordance with these predictions, sting use by *Hadrurus spadix* Stahnke 1940 increased with prey size, reaching 100% once prey items were longer than the scorpion's pedipalp patella length, and with prey activity, which we manipulated by varying prey temperature. Surprisingly, the scorpions were slower to capture less active (cooler) prey than those that exhibited higher rates of activity. We suggest this is because prey are located by vibrations in the substrate, with less active prey producing fewer vibrations.

Keywords: Optimal foraging, venom, pectines

Venom is used by scorpions primarily for capture and digestion of prey and secondarily in defense (Lourenço & Cuellar 1995; Yigit et al. 2007). It is not always used in prey capture however; sometimes only the pedipalps are used (Bub & Bowerman 1979; Polis 1990; Rein 2003), and Rein (1993) has suggested that scorpions sting only if prey resist capture.

Scorpion venom is a complex mixture of low molecular-weight proteins, salts, and various other organic compounds, such as oligopeptides and amino acids (Brownell & Polis 2001). Venom is costly to produce; respirometry studies in scorpions show a marked increase in respiration for some time following ejection of venom from the glands (Nisani et al. 2007). The scorpion *Parabuthus transvaalicus* Purcell 1899 manufactures two forms of venom: a clear pre-venom that contains high levels of salt with very few peptides and a primary venom that contains both salts and high levels of metabolically expensive peptides (Inceoglu et al. 2003). Being more costly to produce, the latter should logically be reserved for the capture of large prey.

Since venom is costly to synthesize and stinging is not obligatory in prey capture, optimization models (Caraco & Gillespie 1986) suggest that venom use should be reserved for prey that cannot otherwise be overpowered. Here we investigate sting use in adult *Hadrurus spadix* Stahnke 1940, a desert-dwelling species from North America, and test the hypothesis that venom is only used on large and/or active prey. *Hadrurus spadix* was chosen for study because its large size makes it easy to observe, and because as an 'equilibrium species' (i.e., species that are slow growing, relatively large, have large broods and are generally of low toxicity (Polis 1990)) it may be representative of the majority of non-buthid scorpion species.

Our experiments were conducted using eight male final (adult) instar *H. spadix* individuals obtained from the wild near Cameron, Arizona, USA by a specialist importer of arachnids (voucher specimen deposited in Cole Museum, University of Reading, UK). Specimens were kept alive in a private collection at the conclusion of the experiments. Pedipalp patella length, correlated with overall length, was used as a measure of size following Benton (1991). Individuals were housed singly in clear Perspex terraria measuring 30 $\times$ 20 $\times$ 15 cm on a 16:8 h light: dark cycle. Light was provided by a single fluorescent tube suspended above the terraria, and temperature was maintained at 27° $\pm$ 2° C during the day and 15° $\pm$ 2° C at night. Mesh lids allowed air circulation with humidity maintained at ca. 50% relative humidity, measured weekly with a hydrostat. A substrate of sand 5 cm deep lined the bottom of each enclosure to allow burrowing, and a single piece of cork bark was added to each terrarium to provide shelter. Water was provided once every two weeks by misting. The prey species used throughout this study was the brown cricket *Acheta domesticus* Linnaeus 1758. The crickets were raised in enclosures kept under identical temperature, light and humidity conditions as the scorpions. They were fed various vegetable matter.

After introducing the scorpions to the terraria we fed them one large (size 1.5, prey sizes are given here as multiples of pedipalp patella length) *A. domesticus* each and then deprived them of further prey for 14 days prior to initiation of the first experiment, which investigated the effects of feeding prey of six different sizes as shown in Fig. 1. We provided each scorpion with a single prey item at each feeding. Feedings occurred twice a week, two hours into the dark photoperiod under red light (scorpions are insensitive to red spectrum light: Machan 1968). We turned on the red light 1 h before feeding and removed the cork bark hides to ensure the scorpions were visible while feeding. We placed prey in the terrarium in the farthest corner from the scorpion and recorded the scorpion's behavior thereafter. Capture time was operationally defined as the time from the alert stance (Bub & Bowerman 1979) until visible movement of the chelicerae was observed, indicating that the prey item was being devoured. A sting was defined as the successful penetration of the prey's exoskeleton by the aculeus. In order to maintain as constant a level of hunger as possible throughout the trial period, we fed the scorpions reciprocal prey sizes in each week's two feedings. For example, the first feeding was of prey of size 1.5, the next feeding was size 0.4, and the following one 1.2. After each of the eight scorpions had been fed all of the six sizes, the whole process was repeated until each scorpion had eaten each prey size three times.

Experiment 2 investigated responses to prey activity. This experiment was started one week after the last, with no food provided in between. We manipulated prey activity by cooling prey in a domestic refrigerator for five, ten or fifteen minutes prior to feeding: the longer the prey had been in the refrigerator, the lower the level of activity displayed (Mellanby 1939). Prey items of size 0.8 were used throughout. Conditions and recording of behavior were otherwise as in Experiment 1. Statistical testing was carried out using Minitab 15.1 (Minitab Inc., Quality Plaza, 1829 Pine Hall Rd, State College, Pennsylvania 16801-3008, USA), controlling for individual differences by entering scorpion identity as a factor where appropriate.

Sting use by the scorpions in Experiment 1 increased when they were offered large prey (Fig. 1, Ordinal Logistic Regression: Z =

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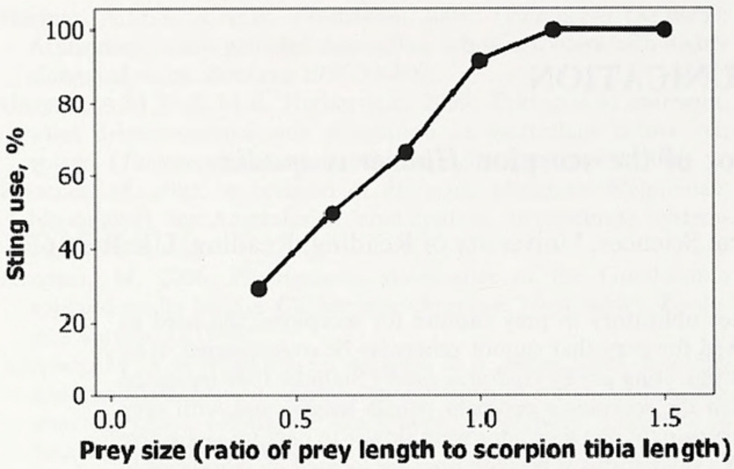

Figure 1.—Sting use by *Hadrurus spadix* increased with prey size. Sting use was measured as the percentage of cases in which the sting was deployed.

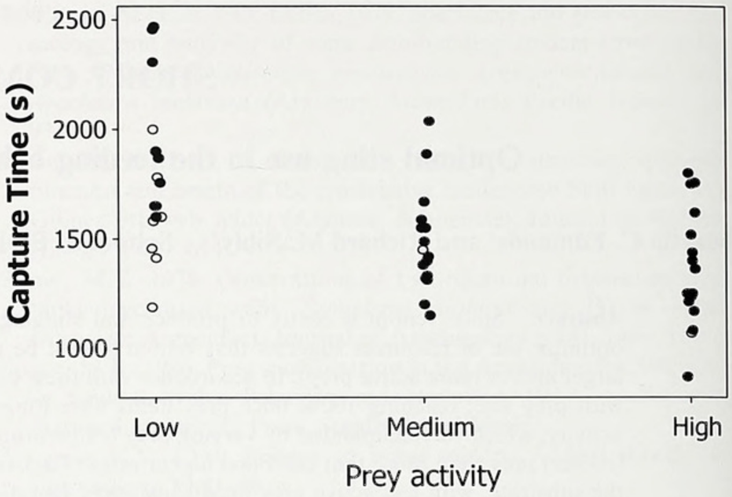

Figure 2.—Capture time and sting use in relation to prey activity. Prey activity was manipulated to be low, medium or high by keeping prey in a refrigerator for 15, 10 or 5 mins, respectively. ● = sting used, o = sting not used. Jitter has been applied to x coordinates to make overlapping points visible.

-4.58, $df = 1$, $P < 0.0005$: the response variable was the proportion of the three trials in which the sting was used). When the smallest prey were offered, stings occurred in only 29% of 24 cases, but this rose to 100% when the prey items were larger than the scorpions' patella lengths. There was no variation in sting use between scorpions ($X_7^2 = 2.37$, $P > 0.05$).

In Experiment 2, prey were rendered less active by keeping them for short periods (5, 10 or 15 min) in a refrigerator. Sting use increased during encounters with more active (i.e., less cooled) prey, as shown in Fig. 2 (Binary Logistic Regression: $Z = -2.70$, $df = 1$, $P = 0.007$). Interestingly, it took longer to catch less active (more cooled) prey (Fig. 2, General Linear Model: $F_{1,15} = 31.3$, $P < 0.0001$). For prey kept in the refrigerator for 15 min, capture time was longer when the sting was deployed than when it was not (General Linear Model: $F_{1,7} = 10.2$, $P = 0.015$). The results are consistent with the hypothesis that sting use is reserved for prey that are difficult to subdue, due to their large size (Fig. 1) or high activity levels (Fig. 2). Less active prey were less likely to be stung and more likely to simply be grasped in the pedipalps. This corresponds to Rein's (2003) suggestion that scorpions sting reluctantly, and only if a prey item struggles, in order to minimize the use of venom and thus its metabolic costs. It is interesting that the sting was invariably used when the prey length exceeded that of the pedipalp patella, suggesting that prey cannot then be reliably held in the pedipalps. Quinlan et al. (1995) reached a similar conclusion from the observation that sting use is more frequent in *Urodacus armatus* Pocock 1888 than in its longer-clawed relative *U. novaehollandiae* Peters 1861.

Surprisingly, the scorpions took longer to capture less active prey items than more active ones (Fig. 2). In situations where prey had not been cooled or had only been cooled for 5 min, the scorpions adopted the alert stance as soon as the prey began to move. When a prey item had been cooled for a greater period of time, however, it took longer to begin moving and/or made reduced movements. In these situations, the scorpions appeared initially ignorant of the presence of the cricket and were slower to locate them once the prey had begun to move. This is consistent with the idea that scorpion species that frequent sandy environments, such as *H. spadix*, locate their prey on the basis of vibrations in the substrate picked up both by their pectines (Brownell, 1977; Mineo & Del Claro 2006) and by the basitarsal compound-slit sensillae of the distal leg segments (Brownell & Farley 1979). The nocturnal scorpion *Smeringurus mesaensis* Stahnke 1957 has been shown to be sensitive to vibrations from a distance of up to 50 cm (Brownell & Farley 1979). By reducing the activity of the prey, there were fewer vibrations in the sand for the scorpions to detect, and this increased capture time (Mineo and Del Claro 2006).

After prey capture, the scorpions were sometimes observed to enter an inactive phase in which they remained motionless with the prey item still grasped in their pedipalps, sometimes for several minutes. This inactive phase is puzzling. Equilibrium species such as *H. spadix* are thought to have evolved low metabolic rates and low levels of surface activity due to constraints placed on them by predation (Polis 1990). By minimizing the period of time required outside of the safety of the burrow, scorpions also minimize their exposure to predators, so it would be logical for scorpions to catch and consume prey as quickly as possible. No function has been suggested for the inactive phase sometimes displayed here (and also reported by Bub and Bowerman (1979) and Rein (2003)), but perhaps the scorpions need to wait for the venom to subdue the prey completely before eating (M. R. Graham, pers. com.).

Wigger et al. (2002) proposed a venom optimization theory to account for the amount of venom injected into prey by spiders. They found that the volume of venom injected into the prey increased with prey size and in prey that were difficult to overwhelm; e.g., in those displaying defensive behavior. These relationships are similar to those reported here. This raises the question, can scorpions control the amount of venom they inject into their prey and thus further conserve this costly resource?

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LITERATURE CITED

Benton, T.G. 1991. The life history of *Euscorpius flavicaudis*. Journal of Arachnology 19:105–110.

Brownell, P. 1977. Compressional and surface waves in sand: used by desert scorpions to locate prey. Science 197:479–482.

Brownell, P. & D. Farley. 1979. Prey localisation behaviour of the nocturnal scorpion *Paruroctonus mesaensis*: orientation to substrate vibrations. Animal Behaviour 27:185–193.

Brownell, P. & G.A. Polis. 2001. Scorpion Biology and Research. Oxford University Press, New York.

Bub, K. & R.F. Bowerman. 1979. Prey capture by the scorpion *Hadrurus arizonensis*. Journal of Arachnology 7:243–253.

Caraco, T. & R.G. Gillespie. 1986. Risk-sensitivity: foraging mode in an ambush predator. Ecology 67:1180–1185.

Inceoglu, B., J. Lango, J. Jing, L. Chen, F. Doymaz, I.N. Pessah & B.D. Hammock. 2003. One scorpion, two venoms: prevenom of

Parabuthus transvaalicus acts as an alternative type of venom with distinct mechanism of action. Journal of Biochemistry 100:922–927.

Quinlan, T.G., G.T. Smith & M.C. Calver. 1995. Relationships between morphology and feeding behaviour in the syntoptic scorpions *Urodacus armatus* and *Urodacus novaehollandiae*. Journal of the Australian Entomological Society 34:277–279.

Lourenço, W.R. & O. Cuellar. 1995. Scorpions, scorpionism, life history strategies and parthenogenesis. Journal of Venomous Animals and Toxins 1:50–64.

Machan, L. 1968. Spectral sensitivity of scorpion eyes and the possible role of shielding pigment effect. Journal of Experimental Biology 49:95–105.

Mellanby, K. 1939. Low temperature and insect activity. Proceedings of the Royal Society of London. Series B, Biological Sciences 127:473–487.

Mineo, M.F. & K. Del Claro. 2006. Mechanoreceptive functions of pectines in the Brazilian yellow scorpion *Tityus serrulatus*: perception of substrate-borne vibrations and prey detection. Acta Ethologica 9:79–85.

Nisani, Z., S.G. Dunbar & W.K. Hayes. 2007. Cost of venom regeneration in *Parabuthus transvaalicus*. Comparative Biochemistry and Physiology 147:509–513.

Polis, G.A. 1990. The Biology of Scorpions. Stanford University Press, Menlo Park, California.

Rein, J.O. 1993. Sting use in two species of *Parabuthus* scorpions (Buthidae). Journal of Arachnology 21:60–63.

Rein, J.O. 2003. Prey capture behaviour in the East African scorpions *Parabuthus leiosoma* (Ehrenberg 1828) and *Parabuthus pallidus* (Pocock, 1895). Euscorpius 6:1–8. Online at http://www.science.marshall.edu/fet/euscorpius/pubs.htm

Yigit, N., A. Bayram & T. Danisman. 2007. Functional morphology of venom apparatus *Euscorpius mingrelicus*. Journal of Applied Biological Sciences 1:27–31.

Wigger, E., L. Kuhn-Nentwig & W. Nentwig. 2002. The venom optimisation hypothesis: a spider injects large venom quantities only into difficult prey types. Toxicon 40:749–752.

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