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Variability in venom volume, flow rate and duration in defensive stings of five scorpion species

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ABSTRACT

Scorpions have been shown to control their venom usage in defensive encounters, depending on the perceived threat. Potentially, the venom amount that is injected could be controlled by reducing the flow speed, the flow duration, or both. We here investigated these variables by allowing scorpions to sting into an oil-filled chamber, and recording the accreting venom droplets with high-speed video. The size of the spherical droplets on the video can then be used to calculate their volume. We recorded defensive stings of 20 specimens representing 5 species. Significant differences in the flow rate and total expelled volume were found between species. These differences are likely due to differences in overall size between the species. Large variation in both venom flow speed and duration are described between stinging events of single individuals. Both venom flow rate and flow duration correlate highly with the total expelled volume, indicating that scorpions may control both variables in order to achieve a desired end volume of venom during a sting.

1. Introduction

Most animal venoms consist of a complex mixture of peptides and proteins in an aqueous medium. The venom components are adapted to alter the target's physiology (Fry et al., 2009; McCue, 2005). These venoms are applied in defense, and for the incapacitation of prey. It is generally accepted that many venomous animals will use their venom frugally, as it can sometimes represent a large metabolic investment, and can take a long time to replenish (McCue, 2006; Nisani et al., 2007; Smith et al., 2014; Wigger et al., 2002). This venom optimization hypothesis has been tested in different groups of venomous animals; for a review, see Morgenstern and King (2013).

Scorpions use their venom defensively against predators, and to immobilize their prey. There are large differences in the defensive use of the stinger between species (Van der Meijden et al., 2013). An ontogenetic shift in stinger use for prey immobilization was reported for two unrelated species of scorpions, *Paruroctonus boreus* and *Pandinus imperator* (Casper, 1985; Cushing and Matherne, 1980), with older specimens using the stinger less. Interestingly, defensive stinging behavior seems to be dependent on body mass, at least in *Centruroides vittatus* (Carlson et al., 2014).

For predation, the Arizona hairy scorpion, *Hadrurus arizonensis*, only uses the venom to immobilize large or struggling prey (Edmunds and Sibly, 2010). Also two *Parabuthus* species have been shown to minimize venom use if it is not necessary to immobilize struggling prey (Rein, 1993). It therefore seems that scorpions optimize their venom expenditure for prey incapacitation. Scorpions that are regenerating their depleted venom have significantly increased metabolic rates, indicating that venom production is a costly process (Nisani et al., 2012, 2007).

Also defensive venom metering has been investigated in scorpions. By pushing the telson through parafilm, and comparing the weight of the scorpion before and after venom expulsion, Nisani et al. (2007) measured venom expenditure in spitting scorpions (*Parabuthus transvaalicus*). Nisani et al. (2012) measured venom mass and protein content of the expelled venom. Nisani and Hayes (2011) found that scorpions under high-threat conditions expel 2.2 times more venom than under low-threat conditions. The scorpions also expelled more opalescent and milky venom, the protein-rich venom that emerges after the clear and pain-inducing "pre-venom" is exhausted, under high threat conditions.

To test the venom optimization hypothesis, the venom expended in defense or prey incapacitation must be quantified.

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Table 1
Measures associated with venom expenditure during stinging per specimen.

Species	*Androctonus amoreuxi*					*Androctonus bicolor*				*Hadrurus arizonensis*					*Hottentotta gentili*		*Smeringurus mesaensis*			
Specimen	Sc2171	Sc2172	Sc2173	Sc2174	Sc2175	Sc1188	Sc1189	Sc1194	Sc2188	Sc1240	Sc1241	Sc1245	Sc1248	Sc1249	Sc1576	Sc1577	Sc2209	Sc2212	Sc2213	Sc2220
Number of stings	5	6	1	3	4	2	2	5	4	2	3	3	3	2	4	3	4	3	1	4
Mean venom volume (μl)	0.681	0.550	0.848	2.127	0.632	0.292	0.303	0.146	0.324	1.488	0.358	0.549	1.301	1.289	0.939	0.088	0.141	0.059	0.049	0.131
Mean injection duration (ms)	269	196	620	583	244	105	158	151	94	197	145	199	307	394	300	150	395	145	142	250
Mean delay before ejection (ms)	20	26	68	46	55	124	236	48	37	57	33	29	168	14	43	31	8	58	8	10
Mean flow rate (μl/s)	2.534	2.803	1.367	3.651	2.590	2.779	1.920	0.969	3.469	7.554	2.472	2.753	4.232	3.273	3.128	0.589	0.356	0.404	0.345	0.522
Mean venom duct area (mm^2)	0.0020	0.0011		0.0018	0.0026	0.0014	0.0016	0.0010	0.0010	0.0013	0.0031	0.0018		0.0020	0.0013	0.0014	0.00018	0.00028	0.00020	0.00021
Mean estimated flow speed (m/s)	0.63	1.30		1.01	0.49	0.98	0.62	0.48	1.80	2.86	0.40	0.74		0.82	1.24	0.22	1.01	0.71	0.86	1.22
Prosoma L (mm)	8.8	9.4		7.4	9.0	9.3	8.4	6.8	8.7	13.5	12.8	11.5	12.6	10.1	11.2	9.2	5.9	6.5	7.3	6.8
Total length (mm)	59.9	66.2		57.7	62.6	71.0	63.7	60.5	59.9	91.7	86.0	81.2	88.8	76.2	85.4	75.4	51.1	53.7	58.0	52.6
Telson length (mm)	9.9	9.8		9.7	10.1	9.2	8.4	6.5	7.3	14.5	12.2	11.1	12.8	11.3	11.2	10.4	6.3	7.0	7.6	7.2