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Mainland versus island differences in behaviour of *Podarcis* lizards confronted with dangerous prey: the scorpion *Buthus occitanus*

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Rapid divergence in behaviour of populations invading novel habitats is often considered adaptive as it may allow a species to exploit novel resources. Here we explore the behavioural response of two closely related species of *Podarcis* lizards living in different habitats, the Spanish mainland and a dry volcanic island, towards a potentially dangerous prey. Our results show that whereas insular lizards attacked scorpions and consequently considered them to be potential prey, mainland lizards tended to flee or ignored them. Sexual differences in the response to scorpions were pronounced in the insular habitat. Males tended to attack scorpions while females tended to ignore them. Inter-specific and inter-sexual differences in the responses of lizards may be mediated by body size differences between populations and sexes. The rapid changes in behaviour allowing insular lizards to recognize scorpions as potential prey may have allowed these animals to capitalize on an abundant food resource in a depauperate environment.

Keywords: poison; feeding; Mediterranean; Columbretes; sexual differences; evolution

Introduction

In habitats with low productivity, insectivorous lizards often consume a high proportion of plants (Colli et al. 1998; Herrel et al. 2004), marine invertebrates (Grismer 1994; Catenazzi and Donnelly 2007), seabird regurgitates, or even resort to scavenging (Castilla et al. 1987). Although most lizards avoid potentially dangerous prey like scorpions, there are some scorpion predators or specialists (McCormick and Polis 1990; O'Connell and Formanowicz 1998, Zlotkin et al. 2003). In arid habitats scorpions can be extremely abundant (Polis 1990) compared with other potential prey, suggesting that behavioural or morphological adaptations that would allow lizards to consume these prey may be selected for in environments with low food abundance.

The endemic lizard *Podarcis atrata* inhabits small islands of the volcanic Columbretes archipelago (Mediterranean, Spain). The islands are characterized by an extreme aridity and by the scarcity of terrestrial insects (Castilla and Bauwens 1991a). Adult lizards consume isopod crustaceans (Castilla et al. forthcoming 2008)

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and scorpions (*Buthus occitanus*) (Castilla et al. 1987), and we have observed the processes of cross predation (i.e., lizards prey on scorpions and scorpions prey on lizards) (Castilla 1995a). In addition, the density of scorpions in the island Columbrete Grande is very high (ca. 0.7 ind/m^2 [Castilla and Pons 2007]). Based on these observations, we expected close ecological interactions between both species on the island.

The archipelago of the Columbretes comprises small (0.5–13 ha) islands whose ages (K-Ar dating) vary from 1 Myr to 8–10 Myr (Aparicio et al. 1991). The islands are situated 51 km east of the Spanish mainland and separated by a channel 90–100 m deep. The islands were connected to the mainland during past glaciations, when the sea level dropped ca. 120 m during the Würm (mid and lower Pleistocene) ca. 20,000 years ago. During that time terrestrial species could have colonized the archipelago from the mainland. Molecular data suggest that the lizard *Podarcis atrata* Boscá, 1916 (previously, *Podarcis hispanica atrata*) colonized the archipelago through the oldest islets (Castilla et al. 1998a and b).

The mainland lizard *Podarcis hispanica* (Steindachner 1870) occupies a large variety of habitats and is common in Spain. It is mainly insectivorous and the consumption of scorpions by this species on the mainland has never been reported (Barbadillo et al. 1999). The taxonomic status of the *Podarcis* group is currently under debate. Based on molecular data there are eight different paraphyletic groups of *P. hispanica* in Spain that have not yet been formally described (Montori and Llorente 2005; Pinho et al. 2006). However, the populations of NE Spain have been included in the group of *P. hispanica* "Type 3" (Pinho et al. 2006) and are closely related to *P. atrata*. The scorpion *Buthus occitanus* (Amoreux 1789) is common in Spain and overlaps with *P. hispanica* in some zones of its range (G. Pons, personal communication), however, very little is known about their interactions in these overlap zones. To our knowledge, no studies have been conducted on the ecology of *B. occitanus* in Spain or elsewhere (Polis 1990), except for some aspects of their feeding behaviour and predation (Leberre 1979; Skutelsky 1995; Skutelsky 1996; Williams et al. 2006).

Scorpions and lizards have occurred together on Columbrete Grande island for at least the last 122 years (Alonso Matilla et al. 1987; present study). However, both species could have been in contact for much longer periods of time. The biogeography and the genetic differentiation between populations of *B. occitanus* from Tunisia, Morocco and Europe is known (Gantenbein and Largiader 2003; Gantenbein 2004; Gantenbein and Keightley 2004; Ben Othmen et al. 2004). However, we lack information about the biogeography and genetic structure of this scorpion species in the Columbretes islands and the Spanish mainland.

On the island, lizards and scorpions share the same rocks as burrows for retreat and protection from predators and weather (own observations). Therefore, although the lizards are diurnal and the scorpions nocturnal, the probability of encounters are high, and we expect interactions between the two species (lizards and scorpions) on the island. On the mainland, the density of scorpions is lower (own observations), and the probability of encounters and interactions is consequently also lower. Moreover, given the lower food abundance on the islands, scorpions may constitute an important food resource there.

The objective of the present study was to compare the behavioural response towards scorpions between the insular lizard species *P. atrata* and the closely related mainland species *P. hispanica*. We examined the willingness of both species of lizards to attack the venomous and potentially dangerous scorpion *Buthus occitanus*. We also explored gender differences in the behaviour of both lizard species, given that they exhibit a pronounced sexual dimorphism in body and head size (Castilla and Bauwens 1991a; Barbadillo et al. 1999).

Materials and methods

Study areas and species

The study was conducted in two distinct areas, one on an island and one on the mainland. The island, Columbrete Grande (13 ha), is located in the Mediterranean (Castellón, Spain, 39°55′N, 0°40′E) (Castilla and Bauwens 1991a). The field work was undertaken during the last week of May 2006 between 10.00 and 13.00 hours under sunny and low wind conditions, allowing appropriate thermoregulation and behaviour of the lizards (Castilla and Bauwens 1991b). The experiments on the island were performed in a vegetated area with a high density of lizards near human habitation where lizards are habituated to human presence (Castilla and Bauwens 1991a). The body size (snout-vent length, SVL) of the lizards tested (*Podarcis atrata*) varied between 60 and 80 mm.

The mainland area was located in NE Spain (Solsona, Lleida, Catalonia, 41°59′N, 1°31′E). The field work was conducted between 10 June and 3 July 2007 between 10.00 and 15.00 hours, under sunny and low wind conditions. The experiments were conducted on rocky walls, bridges gardens and in the river side of the village, where lizards are habituated to human presence. The body size (SVL) of the lizards tested (*Podarcis hispanica*) varied between 45 and 66 mm.

On the island, we captured 12 adult scorpions (body length: 22–26 mm; tail length: 27–30 mm) (Appendix 1). On the mainland, we captured eight adult scorpions (body length: 17–20 mm; tail length: 21–25 mm). All the scorpions were released at their site of capture after the experiments.

Experimental design

To ensure that the lizards were hungry at the time of the experiment we first offered them a mealworm (a preferred prey) attached to a noose. Lizards were not allowed to capture and eat the mealworms to ensure the lizards would be responsive to the scorpion. If the reaction of the lizard to the mealworm was positive (direct attack) we immediately took away the mealworm and offered a scorpion to the lizard.

We used an experimental approach similar to that employed in a previous study conducted on Columbrete Grande to test for the responsiveness of *Podarcis* lizards to potential prey (Castilla and Van Damme 1996). The scorpion was tethered by the base of the tail to a 1m-long nylon thread tied to the end of a pole (Figure 1A). We set the scorpion on the ground 15 cm from the lizard, and recorded the response of the lizard immediately after stimulus presentation. If the response was positive (i.e. the lizard moved towards the scorpion; Figure 1B) the scorpion was moved by the researcher at sufficient speed to keep it near the lizard while preventing capture. If the lizard did not respond to the moving stimulus in 3 minutes we considered it a negative response.

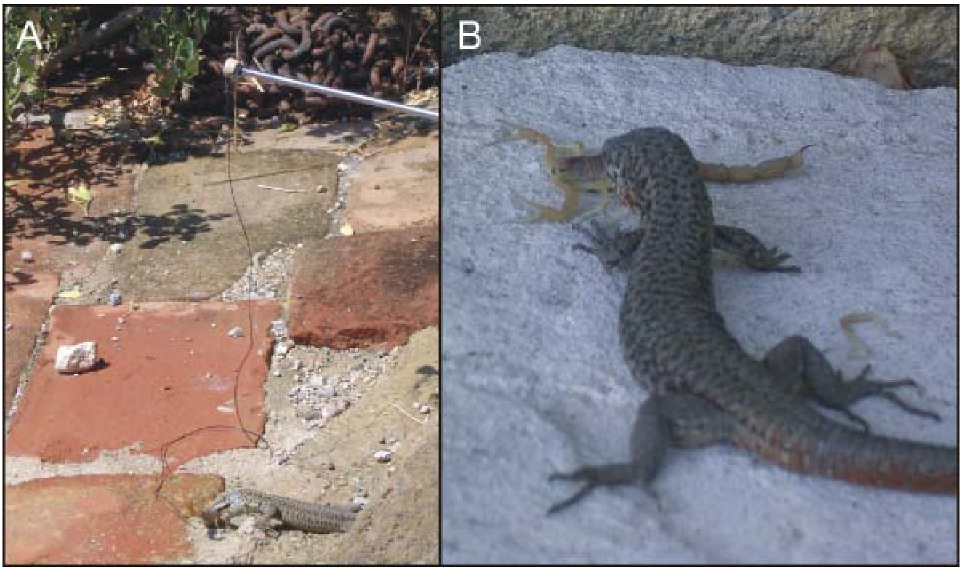

Figure 1. (A) Photograph illustrating experimental set-up. The scorpions were tethered by the base of the tail and placed on the ground about 15 cm in front of the lizards, after which the behavioural responses of the lizard towards the prey were noted. (B) Male *P. atrata* eating a scorpion.

Because we did not capture as many scorpions as the number of lizards tested, the same individual scorpion was used three to five times (Appendix 1). Scorpions rested 6–24 hours between trials in individual enclosures (40×20 cm) provided with sand, stones and food (mealworms and other insects). We tested 41 different adult lizards of both sexes on the island and 30 lizards on the mainland (Table 1). All tested lizards were captured after the experiments with a baited noose (Castilla et al. 1994) and marked with a coloured dot to ensure that they were tested only once. Captured females were checked for gravidity by palpation. On the island, 86% (18 of 21) of females were gravid, while on the mainland 67% (10 of 15) of females were gravid.

Upon presentation of the scorpion to the lizards, we observed the response of the lizard and registered its behaviour. Behaviours were classified as ignore (no response

Table 1. Responses of adult male and female *Podarcis* lizards from different populations towards scorpions (*Buthus occitanus*). Indicated are the sample size (*n*) and relative occurrence of each behaviour (%).

Behaviour	*Podarcis atrata* Island – 2006				*Podarcis hispanica* Mainland – 2007			
	Males		Females		Males		Females	
	n	%	*n*	%	*n*	%	*n*	%
Ignore	8	40	11	52	4	27	2	13
Attack	10	50	1	5	0	0	0	0
Flee	2	10	9	43	11	73	13	87
Total	20		21		15		15	

Table 2. Behaviour of adult lizards towards scorpions of different body size. Percentage (%) of scorpion size relative to the lizard size (see Appendix 1) and number of individuals tested in each case (*n*).

Behaviour	Island				Mainland			
	Females		Males		Females		Males	
	%	*n*	%	*n*	%	*n*	%	*n*
Attack	41	1	32–40	10		0		0
Flee	33–39	9	33–37	2	28–43	13	25–38	11
Ignore	33–42	11	30–40	8	32–40	2	30–36	4

Note: Lizards on the island were confronted with scorpions bigger than on the mainland relative to their body size (mean percentage of 36 vs. 32, respectively).

for 3 minutes), attack (movement of the lizards towards the scorpion) or flee (movement of the lizard away from the scorpion). Differences in response towards the scorpion by lizards of both sexes were compared using chi-squared tests. We used SPSS V.13 (SPSS Inc., Chicago, IL) for all statistical analysis.

Results

On the island, lizards were confronted with scorpions that had a body size (tail excluded) representing 30–42% of the lizard's body size (tail excluded). On the mainland, lizards were confronted with scorpions representing 25–43% of the lizard's body size (Table 2, Appendix 1).

Overall, lizards on the island were confronted with scorpions that were slightly bigger than on the mainland relative to their body size (36% vs 32% respectively) (Table 2). However, insular lizards of both sexes attacked scorpions at a significantly higher proportion (27%; 11 of 41) than mainland lizards. In fact, the mainland *P. hispanica* did not attack any of the scorpions presented (0 of 30; Table 1).

On the island, lizards fled from scorpions that had a mean body size of 23.23 mm (sd=1.44, n=11), ignored scorpions with a mean body size of 24.68 mm (sd=1.60, n=19), and attacked scorpions with a mean body size of 24.55 mm (sd=1.53, n=11). On the mainland, lizards fled from scorpions with a mean body size of 17.97 mm (sd=0.99, n=24), ignored scorpions with a mean body size of 19.30 mm (sd=0.81, n=6), and did not attack any scorpion with a body size between 16.8 and 20.2 mm. The behavioural response of male lizards to the scorpions was significantly different between the two species (χ^2=17.2; df=2; p<0.001). Males of *P. atrata* attacked the scorpions more often and males of *P. hispanica* typically fled from the scorpions. For females, the response was also significantly different between species (χ^2=7.16; df=2; p=0.03), with females of *P. atrata* ignoring the scorpions, and females of *P. hispanica* fleeing more often.

Differences in the response of the two sexes towards the scorpions were significant on the island (χ^2=12.3; df=2; p=0.002) with male *P. atrata* attacking scorpions more often than females. On the mainland, the sexes did not differ in their response to the scorpions and both sexes tended to flee (χ^2=0.83; df=1; p=0.36). In proportion to their body size, female lizards were offered bigger scorpions than male lizards in both study sites (island: female vs male=37% vs 35%; mainland: female vs male=34% vs 31%) (Table 2, Appendix 1).

Discussion

Mainland–island differences

The results of our study show clear and significant differences in the response of insular (*Podarcis atrata*) and mainland (*Podarcis hispanica*) lizards towards the scorpion *Buthus occitanus*. Lizards from the island tended to attack or ignore scorpions, while lizards from the mainland never attacked the scorpions and tended to flee.

Interestingly, a recent molecular study suggests that *P. atrata* is genetically similar to the *P. hispanica* Type 3 from NE Spain (Pinho et al. 2006). However, despite the close genetic similarity, our study shows clear behavioural differences between the mainland and island species. Our findings are not entirely surprising given that both species differ in morphological, physiological, other behavioural and life history characteristics. *Podarcis atrata* is bigger in body size and head size (Castilla and Bauwens 2000), has shorter relative hind limbs and runs more slowly (Bauwens et al. 1995; Van Damme et al. 1998), has a significantly bigger home range (Swallow and Castilla 1996), has smaller clutch sizes relative to body size, and produces bigger eggs (Castilla and Bauwens 2000) compared with *P. hispanica*. Moreover, insular lizards lay communal clutches (while in the mainland they do not [Castilla and Bauwens 1996]), cannibalize eggs and juveniles (Castilla 1995b; Castilla and Van Damme 1996) and consume crustacean Isopoda (Castilla et al. 2007).

At our study site in Catalonia, the density of scorpions is low (own observations), and consequently, encounter rates between *P. hispanica* and *B. occitanus* can be expected to be low. Moreover, food abundance on the mainland is typically higher and thus it is reasonable to assume that lizards would avoid a relatively large and potentially dangerous food item.

Overall, the abundance of scorpions is higher in the arid central and southern areas of Spain than in NE Spain (G. Pons, personal communication). If we assume that the colonization of the Columbretes islands by *Podarcis* hispanica took place from Catalonia (Pinho et al. 2006), then lizards arriving on the Columbretes islands were faced with an abundant, potentially dangerous and "novel" prey. Because the mainland *P. hispanica* did not attack any of the scorpions presented to them but rather fled in their presence, our results suggest that *P. atrata* learned to recognize scorpions as potential prey after they colonized the island.

We know that lizards and scorpions have been coexisting on the island for at least 122 years, based on human observations (Alonso Matilla et al. 1987). Although 100 years were not enough to promote differences in antipredator behaviour against a snake predator (*Vipera latastei*) between *P. atrata* and *P. hispanica* (Van Damme and Castilla 1996), many studies of lizards and other animals have documented recent and rapid divergence in the face of differing habitats and selection pressures (Losos et al. 1997; Herrel et al. 2008). Thus, 100 years should be enough to lead to changes in lizard behaviour towards scorpions and may have facilitated the recognition of scorpions as potential prey for the lizards. Alternatively, the changes in body and head size that occurred after the arrival of the lizards on the islands (Castilla et al. 1987; Barbadillo et al. 1999; Castilla and Bauwens 2000) may have facilitated the inclusion of scorpions as prey into the diet of *P. atrata*.

It would be very interesting to examine the behaviour of *P. hispanica* towards scorpions in arid zones of Spain where the density of scorpions is high and both species share the same habitat to test whether body size evolution has facilitated the consumption of scorpions by *Podarcis* lizards. Given the current trend towards global warming (Reading 2007; Memmot et al. 2007; Massot et al. 2008) with a decrease in rainfall and consequent increase in scorpion densities, future studies should monitor behavioural changes in populations of lizards on the mainland not commonly exposed to scorpions.

Sexual differences

The results of our study show significant gender differences in the response towards scorpions in island species, with males being more willing to attack scorpions than females. However, in proportion to their body size, females were offered bigger scorpions than males. Potentially, the difference in the relative body size of prey could explain the significant gender differences found on the island. Independently of overall body size differences, these results may be a consequence of sexual differences in head size (Castilla and Bauwens 1991a) and bite forces (Herrel et al. 1996; Herrel et al. 2004), which is corroborated by the fact that males on the island also show a higher propensity of cannibalism toward juveniles than females (Castilla and van Damme 1996). Testing females with scorpions with a larger variation in body size could improve our understanding of the observed sexual differences in behaviour.

Most females in this study were gravid during the experiments, this may also have affected their behaviour. Experiments conducted with laboratory rats (Ben Nasar et al. 2007a) and with humans (Ben Nasar et al. 2007b) have demonstrated that the poison of *Buthus occitanus tunetanus* has a stronger effect on pregnant females than on non-pregnant females. It would be very interesting to test the behaviour of *P. hispanica* females during late summer after all clutches have finished, and to compare their tolerance to venom with respect to pregnant females.

Feeding behaviour and poison tolerance

Our study did not focus on feeding or handling behaviour of scorpions by lizards as we did not allow the lizards to consume the attacked scorpions. However, in other lizard species, the foraging repertoire when attacking scorpions often included vigorous shaking of the prey clutched in the jaws, and the throwing of prey from the mouth (O'Connell and Formanowicz 1998). Also, the feeding behaviour of the lizard *Cnemidophorus gularis* differed depending on the size of the scorpion encountered, with a larger number of attacks and more violent attacks directed towards large scorpions compared with small scorpions (O'Connell and Formanowicz 1998).

It is clear that some lizards prey on scorpions, but interestingly scorpions also prey on lizards. In fact, lizards constitute an important part of the diet of scorpions in xeric areas where insect prey are scarce. Several North American and African scorpions of the families *Scorpionidae* and *Buthidae* are predators of diurnal lizards (*Mabuya, Urosaurus, Dipsosaurus, Sceloporus, Uta, Cnemidophorus*) and nocturnal geckos (*Coleonyx, Pachydactylus*, Palmatogecko) (review in McCormick and Polis 1982). Laboratory studies have also demonstrated that scorpions are able to capture successfully, handle and digest lizards (Polis 1990; Zlotkin et al. 2003). Based on such interactions between lizards and scorpions, some adaptations by lizards can be expected including (1) different defensive behaviour; (2) mechanical tolerance (e.g. being morphologicaly impermeable); or (3) metabolic tolerance (Zlotkin et al. 2003).

Our study did not focus on the potential mechanisms that could be adopted by *P. atrata* when facing a scorpion. However, considering the thin skin of the lizards we can assume that mechanical tolerance is rather unlikely. Potentially, the insular *P. atrata* has the ability to tolerate stings or may have learned to handle the prey without being stung. Both possibilities should be tested experimentally. Personal field observations suggest that some adult lizard *P. atrata* can tolerate the poison (unknown dosage) of the scorpion *B. occitanus*. Lizards were sometimes licking the body part where the scorpion had stung them, shook their heads, appeared to be exhausted, and showed temporary paralysis of the hind-legs when stung there. Gekkonid lizards that were injected (1mg crude dry venom per 1g body mass) with the venom of the scorpion *Leiurus quinquestriatus*, showed a similar response (e.g., hind-leg paralysis and reduced breathing rate; Zlotkin et al. 2003).

Finally, it should be noted that adult *B. occitanus* do prey on juvenile *P. atrata* (Castilla 1995a; data from the Natural Park 2007), and adult lizards prey on scorpions. These observations suggest that there must be an ontogenetic shift in lizard behaviour and potentially also in poison tolerance between juvenile and adult lizards. Future studies should be conducted to test the interactions between lizards and scorpions in more detail.

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Appendix 1. Body sizes and behavioural responses of island and mainland individuals

(a) Body size of all island individuals tested and lizard behavioural response.

Sex	Body size *P. atrata* (mm)	Body size *Buthus* (mm)	*Buthus* size as % of *Podarcis* size	Code *Buthus*	Lizard behaviour
gf	61.6	25.1	41	8	attack
gf	66.8	22.1	33	2	flee
gf	68.9	22.8	33	4	flee
f	**63.5**	21.8	34	1	flee
gf	65.0	22.8	35	4	flee
gf	66.4	23.3	35	5	flee
gf	60.3	21.8	36	1	flee
gf	63.8	23.3	37	5	flee
gf	65.3	23.9	37	6	flee
f	**65.7**	25.8	39	10	flee
gf	67.5	22.1	33	2	ignore
gf	62.7	22.1	35	2	ignore
gf	60.5	21.8	36	1	ignore
gf	69.6	26.2	38	12	ignore
f	**68.3**	26.1	38	11	ignore
gf	67.0	25.7	38	9	ignore
gf	64.0	25.1	39	8	ignore
gf	63.2	24.9	39	7	ignore
gf	64.2	25.8	40	10	ignore
gf	62.4	26.1	42	11	ignore
gf	61.4	25.7	42	9	ignore
m	77.6	24.9	32	7	attack
m	69.0	22.2	32	3	attack
m	76.0	25.1	33	8	attack
m	71.5	23.9	33	6	attack
m	66.8	22.8	34	4	attack
m	64.2	22.2	35	3	attack
m	72.5	26.2	36	12	attack
m	69.7	25.8	37	10	attack
m	68.0	25.8	38	10	attack
m	65.4	26.1	40	11	attack
m	66.0	22.1	33	2	flee
m	69.7	25.8	37	10	flee
m	73.0	22.2	30	3	ignore
m	70.1	23.3	33	5	ignore
m	78.7	26.2	33	12	ignore
m	70.2	23.9	34	6	ignore
m	72.6	25.7	35	9	ignore
m	68.2	24.9	37	7	ignore
m	67.9	24.9	37	7	ignore
m	65.9	26.2	40	12	ignore

Note: gf, gravid female; f, female; m, male; non-gravid females are highlighted in bold. Lizards have been ordered according to the relative size of the scorpion offered (see text) within each category of lizard behaviour.

(b) Body size of all mainland individuals tested and lizard behavioural response.

Sex	Body size *P. atrata* (mm)	Body size *Buthus* (mm)	*Buthus* size as % of *Podarcis* size	Code *Buthus*	Lizard behaviour
gf	59.9	16.8	28	1	flee
gf	57.2	17.2	30	2	flee
gf	58.0	17.9	31	4	flee
f	**60.2**	19.3	32	7	flee
f	**56.4**	18.3	32	5	flee
gf	54.3	17.9	33	4	flee
gf	55.7	18.5	33	6	flee
f	**59.7**	20.2	34	8	flee
gf	50.5	17.2	34	2	flee
gf	47.8	16.8	35	1	flee
gf	49.2	18.3	37	5	flee
f	**45.2**	17.6	39	3	flee
gf	46.8	20.2	43	8	flee
gf	57.7	18.5	32	6	ignore
f	**48.0**	19.3	40	7	ignore
m	65.9	16.8	25	1	flee
m	65.4	17.2	26	2	flee
m	63.7	17.6	28	3	flee
m	62.5	17.9	29	4	flee
m	57.2	16.8	29	1	flee
m	60.4	17.9	30	4	flee
m	58.9	17.6	30	3	flee
m	61.2	18.5	30	6	flee
m	55.0	17.2	31	2	flee
m	58.3	19.3	33	7	flee
m	47.6	18.3	38	5	flee
m	64.2	19.3	30	7	ignore
m	66.3	20.2	30	8	ignore
m	56.3	18.3	33	5	ignore
m	55.4	20.2	36	8	ignore

Note: gf, gravid female; f, female; m, male; non-gravid females are highlighted in bold. Lizards have been ordered according to the relative size of the scorpion offered (see text) within each category of lizard behaviour.