The ability of *Aphonopelma steindachneri* (Ausserer) (Araneae: Theraphosidae) to detect and respond to chemosensory cues associated with a predator, *Hogna carolinensis* (Araneae: Lycosidae)

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Summary

This study assessed the ability of second-instar juveniles of the tarantula spider *Aphonopelma steindachneri* to detect and respond to chemosensory cues associated with a naturally-occurring predator, the wolf spider *Hogna carolinensis*. Tarantulas were placed in an arena and presented with a choice between two substrates. One substrate (treatment) contained chemical cues (odours) associated either with *H. carolinensis* or a novel odour associated with a species not likely to be encountered by these spiders (*Tenebrio molitor*). The other substrate was conditioned with water and contained no odour cues (control). In an initial series of experiments, *A. steindachneri* chose the non-conditioned (control) substrates significantly more often than those conditioned by the predator. A second series of experiments showed that responses of *A. steindachneri* were probably due to avoidance of the predator-conditioned substrate, because spiders were observed on the *Tenebrio*-conditioned substrate far more frequently than on the substrate associated with the odour of *H. carolinensis*.

Introduction

It is well known that many species of prey organisms have evolved adaptations associated with detection and defence against predators (see review by Kats & Dill, 1998). These may be morphological, physiological, or behavioural in nature, and often allow prey to assess levels of predation risk (Lima & Dill, 1990; Punzo & Kukoyi, 1997). Chemosensory cues (odours) have been identified from the integument and faeces of many vertebrate and invertebrate predators, and prey organisms can use odours associated with these chemicals to avoid them (Punzo, 2002). The ability of prey to detect such cues may be a function of cognitive or genetic (innate) mechanisms (Barreto & Macdonald, 1999; Punzo, 2000). Most research on this topic has been conducted on aquatic vertebrates and insects (Kats & Dill, 1998) as well as terrestrial reptiles and mammals (MacDonald & Müller-Schwarze, 1990).

In contrast, far fewer data are available for arachnids, with most studies focusing on spiders belonging to the suborder Araneomorphae. For example, the linyphiid *Frontinella pyramitela* (Walckenaer) is capable of responding to chemosensory cues (odours) associated with the cuticle of araneid predators (Suter *et al.*, 1989). The lycosid *Pardosa milvina* (Hentz) reduces locomotor activity and avoids substrates containing odours associated with the silk and faeces of larger lycosid predators (Persons *et al.*, 2001; Walker & Rypstra, 2003). *Oxyopes salticus* Hentz (Oxyopidae) can recognise chemosensory cues associated with predators and prey (Punzo, 2002).

Hogna carolinensis (Walckenaer) is amongst the largest species of lycosid in the USA, and frequently captures and ingests juvenile stages of theraphosid spiders (tarantulas) in areas where both species are sympatric (Punzo, 2003). This lycosid may hunt during the day or night, depending on the location and season, and feeds on a variety of arthropod prey types (Shook, 1978). Juveniles and adults of *H. carolinensis* can be found standing motionless or wandering over the ground surface, within rock crevices, or under logs and other plant debris (Gertsch, 1979). These spiders frequently excavate shallow burrows often topped with turrets constructed of silk, leaves and blades of grass (Punzo, 2000).

To my knowledge, no studies have been conducted to determine whether spiders belonging to the suborder Mygalomorphae can detect and respond to odours associated with predators. The tarantula spider *Aphonopelma steindachneri* (Ausserer) (Araneae, Mygalomorphae: Theraphosidae) is found in the northern region of the Chihuahuan Desert in the southwestern U.S. (Smith, 1995; Breene *et al.*, 1996). Tarantulas are generalist predators and, like lycosids, also feed on a variety of arthropods, while also adding small vertebrates to their diet (Baerg, 1958; Punzo & Henderson, 1999). Common arthropod predators of *A. steindachneri* include pepsine spider-wasps of the genus *Pepsis* and *Hemipepsis* (Williams, 1956; Cazier & Mortenson, 1964; Punzo, 1994), as well as centipedes, scorpions, solifugids, and lycosid spiders (Punzo, 1998, 2000).

The purpose of this study was to determine whether juveniles of *A. steindachneri* will avoid substrates containing odours associated with *Hogna carolinensis*, which occurs sympatrically with *A. steindachneri* in Pecos County, Texas, USA. Juveniles were chosen as subjects because they typically move over the surface of the ground in search of shelter sites (Baerg, 1958; Punzo & Henderson, 1999), have a body size that makes them vulnerable to several juvenile stages of *H. carolinensis*, and are thus likely to encounter chemosensory cues left by this lycosid as it moves about the surface or waits in ambush for suitable prey.

Material and methods

Individuals of *A. steindachneri* and *H. carolinensis* were captive-bred offspring from parents originally collected in Pecos County, Texas during March and April of 2001. Spiders of each species were housed in separate rooms and were maintained individually in plastic cages (16 × 15 × 12 cm) at 22–23°C and 60–63% relative humidity in Percival Model 85A environmental chambers (Boone, Iowa). Juvenile and adult spiders were provided with water *ad libitum*, and adults were fed twice per week on a diet consisting of nymphs of cockroaches (*Periplaneta americana*), crickets (*Acheta domesticus*), and ground beetles (*Carabus* spp.). The diet of juvenile tarantulas consisted of fruitflies (*Drosophila mojavensis* and *D. melanogaster*) as well as first-instar nymphs of crickets. All cages housing spiders were provided with vermiculite as a substrate.

Vermiculite from cages housing *H. carolinensis* was used as a source of chemosensory cues (odours) in these experiments. All tarantula spiders used as subjects were second-instar juveniles (7 days old) and were considered "naive" because they had no previous experience with *H. carolinensis*.

Experiments were conducted in a plastic test chamber (20 × 20 × 10 cm). Each half of the chamber floor was covered with a sheet of absorbent paper. One of the papers was soaked in aged tap water without any animal-associated chemosensory cues (control paper). The other sheet was obtained from paper that had been placed on the vermiculite in cages housing *H. carolinensis* for a period of one week before testing (treatment paper), thus containing odour cues associated with this wolf spider. This paper was also soaked in aged tap water to ensure that subjects were responding to odours and not differences in moisture content of the paper.

In the first series of experiments, individuals of *A. steindachneri* ($n=25$) were placed in the centre of the chamber at the interface between both sheets of paper. The position of each subject was recorded at 3-min intervals over a period of one hr, resulting in 20 observations for each spider. If an animal's body was in the middle of the chamber, the position of the pedipalps was used as an indicator of substrate preference. The chamber was thoroughly cleaned after each trial with a soapy sponge and new sheets of paper introduced. Each subject received one trial and the position of the control and treatment papers was switched after each trial, using a table of random numbers, to avoid any position effect.

In these experiments, any preference exhibited by subjects could be attributed to a choice between a substrate containing odours versus one that did not (rather than a response specifically to a lycosid odour). Hence, a second series of experiments were conducted in which I replaced the control paper (no odour) with a sheet of paper that had been allowed to stand in cages housing a laboratory colony of mealworm beetles (*Tenebrio molitor*). This represents a novel odour associated with a species not normally likely to be encountered by *A. steindachneri*. Thus, if tarantula spiders are capable of responding to predator odour cues (*H. carolinensis*), then it was hypothesised that they would prefer odour cues associated with a non-predator to those of a lycosid spider. Papers containing odours associated with *T. molitor* were also soaked in tap water as described above for *H. carolinensis*.

The same 25 spiders were used in both series of experiments, with an interval of two days between them. For all experiments the chamber was placed in a temperature-controlled room (22 ± 0.3°C, 60–63% RH, 12L:12D photoperiod regime). The number of observations of test subjects on control substrates was compared with that expected on the basis of an even distribution in the chamber (10 out of 20 observations per subject), using one-tailed Wilcoxon matched-pairs tests (Sokal & Rohlf, 1995).
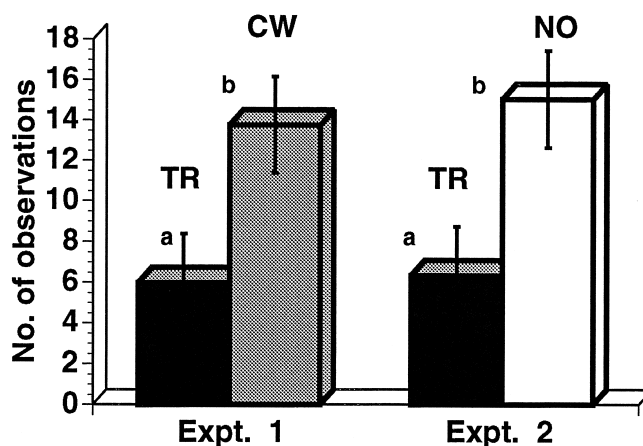

Fig. 1: Mean numbers of observations of juveniles of *Aphonopelma steindachneri* on substrates marked by various chemosensory cues. Experiment 1: substrates marked with predator (treatment) odour (TR) (*Hogna carolinensis*) versus control (water, CW). Experiment 2: predator (treatment) odour (TR) (*H. carolinensis*) versus novel odour (NO) associated with *Tenebrio molitor*. Vertical bars represent ± SE, $n=25$ per group. Same animals used for both experiments. Bars with different letters are significantly different, $p<0.003$ (Wilcoxon matched-pairs test).

Results and discussion

In experiment 1, juveniles of *A. steindachneri* chose the non-conditioned (control) substrates significantly more often than those conditioned by the predator *H. carolinensis* (Fig. 1; $T=348.2$, $p<0.003$). Experiment 2 showed that the responses of *A. steindachneri* were probably due to the avoidance of the predator-conditioned substrate, because spiders were observed on the *Tenebrio*-conditioned substrate far more frequently than on the substrate associated with the odour of the predator *H. carolinensis* (Fig. 1; $T=365.7$, $p<0.003$).

These results show that juveniles of *A. steindachneri* avoid substrates containing chemosensory cues associated with a naturally-occurring predator. This response cannot be explained merely in terms of a simple avoidance of a novel stimulus, because the spiders preferred a substrate conditioned by *Tenebrio* odour cues over one conditioned by *H. carolinensis*. Furthermore, this avoidance response of *A. steindachneri* appears to be innate because spiders were reared in captivity and thus had no previous exposure to *H. carolinensis*. This also suggests that the behaviour is adaptive and that *A. steindachneri* may have the ability to detect and avoid sites frequented by its predators, which would presumably increase overall fitness.

Although many lycosids may use a sit-and-wait strategy when hunting, juveniles and adults can move considerable distances during their lifetime, changing their locations in response to prey abundance (Cady, 1984). *Hogna carolinensis* is often observed wandering over the ground surface or seeking refuge under rocks, and is sometimes found in shallow burrows (Farley & Shear, 1973). During this type of locomotor activity, these spiders leave their own chemical signatures on the ground. Juvenile tarantulas begin to wander over variable distances in search of food or shelter sites such as

burrows and rock crevices (Minch, 1979; Punzo & Henderson, 1999). The results of these experiments indicate that juvenile tarantulas are capable of detecting and subsequently avoiding substrates that contain chemosensory cues associated with *H. carolinensis*, which represents a common predator of juvenile tarantulas in the southwestern United States.

It has been suggested that prey organisms should have the ability to assess accurately the risk of predation and respond in a graded manner according to the level of threat posed by a predator (threat-sensitivity hypothesis; Helfman, 1989). Animals that exhibit antipredator responses to non-threatening stimuli expend energy that could be allocated toward other activities such as courtship and mating, reproduction, and finding food. In contrast, animals that fail to respond to threatening stimuli reduce their chances of survival.

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