Response of the solifugid *Eremobates marathoni* Muma & Brookhart (Solifugae, Eremobatidae) to chemosensory cues associated with a common prey organism

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Summary

In this study I investigated the ability of second-instar nymphs of the solifugid Eremobates marathoni (Arachnida, Solifugae: Eremobatidae) to detect and respond to chemosensory cues associated with a naturally-occurring prey species, Dicaelus costatus (Coleoptera: Carabidae). Solifugids were presented with a choice between two substrates in a test chamber. One substrate was conditioned with water and contained no odour cues (control), while the other substrate contained either odour cues associated with D. costatus or a novel odour associated with an insect not likely to be encountered by whipscorpions (Tribolium confusum). In an initial series of experiments, E. marathoni chose the prey-conditioned substrates significantly more often than control substrates. A second series of experiments showed that the responses of E. marathoni were probably due to active selection of the prey-conditioned substrate, because solifugids were observed on D. costatusconditioned substrates far more frequently than on substrates conditioned with T. confusum. Because solifugids were captive-bred and had no previous experience with D. costatus, their response to chemical cues associated with this beetle appears to be innate.

Introduction

The sensory adaptations used by predators to locate prey are diverse and can vary with foraging tactics and microhabitat characteristics (Punzo & Gonzalez, 2003). Cues commonly used to detect prey can be mechanical, visual, or chemical in nature (Brown, 1989). The ability to use chemosensory stimuli to detect prey has been observed in vertebrate (Punzo, 2003, 2004) and invertebrate (Chapman *et al.*, 1987) predators. Among invertebrates, most research has focused on gastropod snails (Duval *et al.*, 1994) and insects (Lima & Dill, 1990). With respect to arachnids, spiders have received most of the attention, while few data are available for other arachnid taxa (Punzo & Preshkar, 2002).

To my knowledge, no one has investigated whether or not solifugids (Solifugae) can detect and respond to odours associated with prey organisms. *Eremobates marathoni* Muma & Brookhart is a common component of the arachnid fauna of the northern Chihuahuan Desert in the southwestern USA (Punzo, 1998a). It is a generalist predator and feeds on a variety of arthropod prey types (Punzo, 1998b). The purpose of this study was to determine whether nymphs of *E. marathoni* can detect and respond to chemical (odour) cues associated with the beetle *Dicaelus costatus* LeConte (Coleoptera: Carabidae), a species that is frequently captured and eaten by this arachnid (Punzo, 2000).

Material and methods

Dicaelus costatus occurs sympatrically with E. marathoni in Big Bend Ranch State Park (BBRSP, Presidio Co., Texas). All subjects (E. marathoni and D. costatus) were captive-bred offspring from parents originally collected in BBRSP (within a 0.5 km radius of Presidio, Texas) during May and June 2002. They were housed individually in plastic cages $(15 \times 12 \times 10 \text{ cm})$ that were placed in a Precision Model 85A environmental chamber at 23°C, 60-62% relative humidity, and on a 12L:12D photoperiod regime. Solifugids and beetles were provided with water ad libitum, and fed once per week on a diet consisting of mealworm beetle adults and larvae (Tenebrio molitor), as well as nymphs of cockroaches (Periplaneta americana) and crickets (Acheta domesticus). All E. marathoni used in these experiments were second-instar nymphs (3.5-4.0 mm in length), and were "naive" in that they had no previous experience with D. costatus. Second-instar nymphs were chosen as subjects because under natural conditions earlier postembryonic stages (protonymphs and firstinstar nymphs) are sedentary and do not feed (Punzo,

1998a). When first-instar nymphs moult, the resulting second-instar nymphs leave their nest and begin to hunt and feed (Punzo, 1998b). All cages housing *D. costatus* and *E. marathoni* were provided with a substrate consisting of vermiculite.

Experiments were conducted in a plastic test chamber $(17 \times 17 \times 7 \text{ cm})$ in a room with the following environmental conditions: 22–24°C, 60–65% relative humidity, 12L:12D photoperiod regime. Each half of the chamber floor was covered with a sheet of brown absorbent paper. For one week before testing, one of the papers was placed in a separate container and covered with fresh vermiculite that did not contain any animal-associated chemosensory cues (control paper). The other sheet was obtained from paper that had been placed (conditioned) for the same amount of time in vermiculite obtained from cages housing *D. costatus* (treatment paper), thus containing odour cues associated with this beetle. All subjects were deprived of food for one week before testing.

In the first series of experiments, individual solifugids (n=35) were placed in the centre of the chamber at the interface between both sheets of papers. I then recorded the position of each subject at 3-min intervals over a period of one hr, resulting in 20 observations for each solifugid. If an animal's body was in the middle of the chamber, I used the position of the pedipalps as an indicator of substrate preference. The chamber was thoroughly cleaned after each trial and new sheets of paper introduced. Each solifugid was tested only once, and the position of control versus treatment papers was changed for every trial using a table of random numbers to avoid any position effect.

In the preceding 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 beetleassociated odours). Thus, following the procedures described above, 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 flour beetles (Tribolium confusum). This represents a novel odour derived from a species not likely to be encountered by E. marathoni. Thus, if solifugids are capable of responding to prey chemosensory cues (beetle), then I predicted that they would prefer odour cues associated with a prey animal (D. costatus) to those of a non-prey animal.

The same 35 solifugids were used in both series of experiments, with an interval of two days between them. 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).

Results and discussion

Two subjects exhibited abnormal locomotor movements (legs intermittently buckling during experimen-



Fig. 1: Mean (\pm SE) number of observations of 2nd-instar nymphs of *Eremobates marathoni* on substrates conditioned with control (CO) versus prey odour (PR) (**A**-first series of experiments), and on substrates conditioned with prey (PR) versus novel odour of a non-prey insect, *Tribolium confusum* (NO) (**B**-second series of experiments). All subjects (*n*=35) were tested only once in each experiment. Bar graphs with different letters (a, b) are significantly different, *p*<0.001.

tation) in the first series of experiments, and were not included in the data analysis. In these experiments, *E. marathoni* chose the prey-conditioned substrates (Fig. 1A, PR) significantly more often than the control (CO) substrate (T=275.2, p<0.001). The second series of experiments (Fig. 1B) showed that the responses of *E. marathoni* were probably due to the selection of prey-conditioned substrate, because solifugids were observed on *D. costatus*-conditioned substrates (PR) far more frequently than on substrates associated with the novel odour of *T. confusum* (T=309.1, p<0.001).

These results show that second-instar nymphs of E. marathoni are capable of detecting and responding positively to substrates containing chemosensory cues associated with naturally-occurring insect prey. This response is not merely a function of being attracted to an odour stimulus per se, because the solifugids preferred a substrate conditioned by prey odour cues over one conditioned by T. confusum. In addition, their response appears to be innate rather than learned because the solifugids were captive-bred and had no previous exposure to *D. costatus*. This also suggests that the behaviour is adaptive and that *E. marathoni* may possess the ability to detect and position itself on sites frequented by this beetle. The beetle presumably leaves a chemical signature on the substrates that it visits during its foraging activities, and E. marathoni can respond to these chemosensory stimuli. This might affect patch residence time, with E. marathoni concentrating its own foraging bouts on chemically-marked substrates, thereby increasing the probability of encounter with a suitable prey species. As a result, hunting success may be enhanced and overall fitness should increase.

The ability of *E. marathoni* to detect and respond to chemical stimuli associated with prey is in agreement with data reported for some species of spiders (Araneae). For example, naive wolf spiders (*Hogna carolinensis* (Walckenaer)) responded to chemical stimuli associated with prey such as field and house crickets

(Punzo & Preshkar, 2002). Lynx (*Oxyopes salticus* Hentz) and wolf (*Trochosa parthenus* (Chamberlin)) spiders recognised chemical cues associated with prey organisms, and spent significantly more time in patches containing odour cues left by *Schistocerca obscura* (Orthoptera: Acrididae), a naturally-occurring prey species (Punzo & Kukoyi, 1997). The gradual diminution of prey-associated chemical stimuli, as a result of decreasing numbers of prey, may be used by predators to assess patch quality and to make decisions on when to switch to other patches.

In conclusion, predators that are able to detect and respond to prey-associated chemical stimuli, either innately or through experience, should increase their probability of successfully capturing prey and increase energy assimilated into body tissues. This, in turn, should increase fecundity and overall fitness.

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