SHORT COMMUNICATION

THE SPIDER ENOPLOCTENUS CYCLOTHORAX (ARANEAE, CTENIDAE) AVOIDS PREYING ON THE HARVESTMAN MISCHONYX CUSPIDATUS (OPILIONES, GONYLEPTIDAE)

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ABSTRACT. Field observations suggested that the spider *Enoploctenus cyclothorax* (Bertkau 1880) avoids preying on the harvestman *Mischonyx cuspidatus* (Roewer 1913). The objectives of this study were to test the degree to which this prey avoidance occurred, and to test the effects of starvation on predation rates. Laboratory prey-predator encounters showed that 77.8% of the spiders rejected the harvestmen even after severe starvation, dying after sharing the same terrarium with a harvestman for 68.6 \pm 21.8 days. Two spiders fed on the harvestmen, but only after one week. In comparison, crickets given to the control group were all consumed after 13 hours. Prey recognition and subsequent avoidance, without conspicuous exudation of the scent glands (92.9% of the cases), occurred only after the harvestman was touched. We conclude that adult *E. cyclothorax* do avoid preying on *M. cuspidatus*, even after severe starvation, suggesting that the latter is recognized by the former by its chemical properties.

Keywords: Opiliones, Ctenidae, prey avoidance, prey detection, distasteful

Spiders of the family Ctenidae are medium to large wandering spiders that typically inhabit forests (Gasnier & Höfer 2001). They hide during the day in natural retreats including holes in tree trunks and under the base of strong and large leaves of bromeliads, palms and others (Barth et al. 1988; Höfer et al. 1994). At night, they leave their retreats and wait for prey (Salvestrini & Gasnier 2001), which includes a large variety of arthropods (Barth & Seyfarth 1979; Höfer et al. 1994). However, ctenid spiders as a whole apparently do not feed on every prey they are able to subdue (see Nentwig 1986). Willemart and Kaneto (2004) observed adult female Enoploctenus cyclothorax (Bertkau 1880) attacking the laniatorid harvestman Discocyrtus sp. (Opiliones, Gonyleptidae) but moving back without biting after touching it with their first legs, even though the harvestmen never reacted aggressively. If E. cyclothorax actually avoids preying on a harvestman species, the latter could be added in the list of arthropods rejected by many spiders, such as some species of stinkbugs, ants, caterpillars and others (Foelix 1996). This study aimed to determine if adult E. cyclothorax avoids preying on a co-occurring harvestman and whether this prey avoidance behavior is associated with food deprivation (see Gelperin 1968).

Eighteen adult females of E. cyclothorax (length [total/cephalothorax]: $\sim 20.0/9.0$ mm), nine adult males of the harvestman Mischonyx cuspidatus (Roewer 1913) (dorsal scute length: ~ 5 mm) and nine adults of Endecous betariensis crickets (Phalangopsidae) (body length: ~ 15.0 mm) were used in the experiments. The spiders and the harvestmen were collected at night, in the Reserva da Cidade Universitária Armando de Salles Oliveira (C.U.A.S.O.), city of São Paulo (state of São Paulo), southeastern Brazil (23°33'S, 46°43'W), a well developed secondary forest. The crickets were collected in the Parque Estadual Turístico do Alto do Ribeira (PETAR), an Atlantic forest reservation in São Paulo state, southeastern Brazil (cave location: 24°32'57"S, 48°43'15"W), and were brought to the laboratory in vials. The crickets were transferred from the latter directly to the "cricket group" terrarium (see below). Voucher specimens were deposited at the Museu de Zoologia da Universidade de São Paulo (MZUSP).

Spiders were individually housed in clear plastic containers (20 $1 \times 10 \text{ w} \times 10 \text{ h}$, cm) with damp soil on the bottom, and maintained at 25° C. In the first experiment, spiders were fed to satiation for 8–10 days (d) before the starvation period started by offering immature laboratory reared cockroaches

(*Periplaneta americana*, Blattidae) and adult laboratory reared crickets (*Gryllus gryllus*, Gryllidae) *ad libitum*. Harvestmen were fed on larval pieces of the beetle *Tenebrio molitor* (Tenebrionidae), boiled rice and water soaked bread and maintained in another laboratory where temperature was not controlled. *Endecous betariensis* crickets have been used as a comparison group in the experiment of prey-predator encounter. It was chosen for being a different species from the cricket used to feed the spiders, thus avoiding prey species recognition that could possibly influence the capture rate (see discussion in Curio 1976).

Nine spiders were randomly chosen to be tested with crickets and the other nine to be tested with harvestmen. Both groups were deprived of food 21 d before testing to maximize the possibility that they would be hungry. During the night period at 25° C in a darkened room, each spider of the "cricket group" was offered one E. betariensis cricket, whereas each spider of the "harvestman group" was offered one M. cuspidatus harvestman. Crickets and harvestmen were introduced in the terraria where the spiders were being maintained. Prey was placed as far from the spider as possible to create a more realistic situation in which the latter could detect the prey from a distance. We observed the spiders continuously during one hour, all at the same time (two observers; no predation events occurred simultaneously). In the following days, we checked whether the spiders preyed on the harvestmen/crickets once each 1-2 d, between 11:00 and 15:00 h, until either the harvestmen/crickets were eaten or the spiders died. As there were no retreats in the terraria, the prey could not hide from the spiders. Once a week, we fed the harvestmen (in the spider's terraria), with soaked bread or rice, items chosen because they would probably not be of interest to the spiders. These items were introduced in front of the harvestmen (< 1 cm away), thus allowing immediate feeding, and removed the following day to avoid fungal proliferation.

While checking the tested individuals every 1–2 d, we noted the position of prey and predators. Because the cover of the terrarium was divided by grids into six equal parts, we could conduct two analyses to infer mobility of both spiders and harvestmen in each terrarium (moving would facilitate mutual perception and therefore predation—see Barth 1982). We counted how many times each individual was in each section of grid, and how many times they moved from one part to another.

In a second experiment we investigated the physical interactions between spiders and harvestmen by conducting prey-predator encounters. Eleven adult or subadult *M. cupidatus* (5 females and 6 males) and 11 adult females *E. cyclothorax* were collected in the C.U.A.S.O. and brought to the laboratory. Spiders were maintained in the same conditions

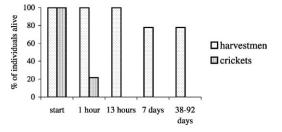


Figure 1.—Comparative predation rate by adult spiders *Enoploctenus cyclothorax* on the harvestmen *Mischonyx cuspidatus* and the crickets *Endecous betariensis*. The x-axis is time after the start of the tests.

mentioned above and deprived of food 21 d before each of the harvestmen were introduced in a spider terrarium, also as described above. We monitored each pair (the spider and the harvestman of each terrarium) continuously, at the same time (two observers, no predation events occurred simultaneously), until all the pairs had made physical contact and shortly thereafter. Our intention was to better describe at what point the spider avoided the harvestman (before or after contact), whether or not the spiders bit, and the harvestmen's defensive behavior. Data are presented as means \pm standard deviation.

Within the first hour of the first experiment, seven out of nine crickets were consumed, and none of the harvestmen were preved upon (Fisher exact test: P = 0.002) (Fig. 1). After 13 h from the beginning of the experiment, all crickets were eaten. Only after 7 d were the first two harvestmen eaten (i.e., 28 d after the spiders had last eaten [Fig. 1]). The two spiders that fed on the two harvestmen were kept in the terrarium, fed on G. gryllus once per week but died 11 and 33 d after eating the harvestmen (i.e., 18 and 40 d after the introduction of the harvestmen in their terraria). The other seven spiders kept with harvestmen without consuming them died 68.6 \pm 21.8 d (n = 7; range = 38–92 d) after the harvestmen were introduced in their terraria (Fig. 1). After the first day of the experiment, spiders of the "cricket" group (which ate one E. betariensis and then one G. gryllus per week) died after 57.3 \pm 28.6 d (n = 6; range: 14–95 d). There was no difference between the survival of spiders of the "harvestmen group" that did not consume the harvestmen and spiders of the "cricket group" (*t*-test: t = 0.804; P = 0.438; df = 11).

Both the harvestmen and the spiders were seen in almost all parts of the terraria and did move between these parts (changes from one of the six parts to another, in percentage of observations: spiders $66.4 \pm 10.5\%$; harvestmen: $46.7 \pm 7.6\%$), and so we assumed they perceived each other (Fig. 2).

Below we present data from the 11 observations

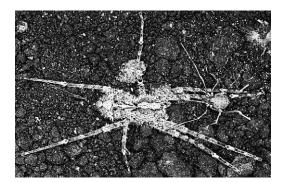


Figure 2.—An adult spider *Enoploctenus cyclo-thorax* showing no interest in the harvestman *Mischonyx cuspidatus*. Spider total length (cephalothorax + abdomen = \sim 2 cm). Picture by R. de Andrade.

of the second experiment plus three observations done with the "harvestman group" in the first experiment. In ten out of 11 observations, the spiders touched the dorsum of the harvestmen (with the ventral parts of their legs I and/or II and/or III and/ or dorsum of the pedipalps) but retreated upon contact. Once, a spider gently carried a male harvestman forming a basket with legs I and pedipalps, then touched it with the mouth without biting, and finally released the prey. In another occasion the spider touched the harvestman's body with leg I, then bit its leg II and retreated thereafter. Once, a spider attacked the harvestman from a 5 cm distance (tip of the spider leg to the harvestman's body), but the harvestman managed to flee by running. No further contact was made.

In these 13 observations, the harvestmen did not release visible secretions from their scent glands and either remained motionless (n = 10) or kept walking slowly when contacted by the spiders (n = 3).

In only one case did the spider bite the harvestman's body. The spider gently carried the harvestmen with legs I and the pedipalps and bit the anterior region of its body. After holding it for three seconds, the spider released the harvestman and rubbed the dorsal region of her pedipalps and the anterior region of the body on the ground. At some point the harvestman released secretions from its scent glands since a characteristic odor spread out of the terrarium. Both the harvestman and the spider lived at least 30 d after the encounter.

The choice of prey by predators is expected to involve energetic values of prey, manipulation time (Elner & Hughes 1978; but see also Meire & Ervynck 1986), searching time (Krebs et al. 1977), and palatability (Eisner 1970). In turn, prey have developed several mechanisms used to deter predators, be they morphological, behavioral, chemical,

or a combination of these features (see Edmunds 1974). There is no reason to believe that harvestmen provide so much less energy that it would not be worth to feeding on them after a long starvation period as other harvestmen are preyed on by several other organisms including spiders (see e.g., Machado et al. 2005). The harvestmen never used mechanical defenses that would require the need of any specific manipulation. Because ctenid spiders bear strong chelicerae, we also have no reason to believe that they would have to manipulate the prey to search for softer parts of the cuticle. Moreover, Willemart & Kaneto (2004) reported two individuals of E. cyclothorax feeding on two distinct harvestmen, which were left in pieces. Finally, searching time was minimal in our experiment. Both the spiders and the harvestmen moved in the small terrarium (Fig. 2) and there were no possible hiding places. Therefore, we must look for other reasons that would cause M. cuspidatus to be avoided by adult E. cyclothorax.

One possibility is that mechanical defense, such as bites with the chelicerae, pinching with the spiny pedipalps, or nippings with the fourth pair of legs (e.g., Gnaspini & Cavalheiro 1998) of the harvestmen inhibit attack by the spider. However, none of these behaviors were observed when the spiders touched, carried, or bit the harvestmen (as also observed by Willemart & Kaneto 2004). The possibility that rapid movement by the harvestman prevented the spiders from catching this prey can be empirically rejected since this rapid avoidance by the harvestman was only observed once in 12 observations, and in an exceptional case in which the spider did not wait for a closer range attack. We are left with the possibility of unpalatability, that a chemical defense provokes the rejection by the spider. Acosta et al. (1993) reported a thin and hardly detectable layer of scent gland secretions in the lateral grooves of resting Pachyloidellus goliath (Acosta 1993). This could result from release of small amounts of secretion or could be residual from previous exudations; either way it is possible that visually inconspicuous repellents were secreted by the test harvestmen in this study. Another possibility is that the tegument contains chemicals that are repellent to some predators (see Eisner et al. 2004; Machado et al. 2005). Therefore, even when no visible secretions are released, harvestmen may be chemically protected.

Because, in 13 observations, the spiders moved over the harvestmen and retreated only after touching them, we can infer that, although detection of the harvestmen occurred at a distance, recognition and rejection were only possible after contact. As discussed above, the chemical properties of the harvestmen, and not mechanical ones (such as size and texture), are probably mediating this recognition, since the former is more specific than the latter (see Van Loon & Dicke 2001). Chemical recognition would be mediated by contact chemoreceptive hair sensilla, which are typically present mainly on the distal parts of the legs and pedipalps (e.g., Barth 2002).

Because of the small number of observations, we cannot speculate on why the two spiders that ate the harvestmen died sooner. Finally, we should note that feeding on crickets or not feeding at all did not result in differences in survival times among spiders, suggesting that death was not related to starvation and thus the latter did not play a role in increasing a spider's likelihood of consuming a harvestman.

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LITERATURE CITED

- Barth, F.G. 1982. Spiders and vibratory signals: sensory reception and behavioral significance. Pp. 67–122. *In* Spider Communication: Mechanisms and Ecological Significance (P.N. Witt & J.S. Rovner, eds.). Princeton University Press, Princeton, New Jersey.
- Barth, F.G. 2002. A Spider's World: Senses and Behavior. Springer Verlag, Berlin. 394 pp.
- Barth, F.G. & E-A. Seyfarth. 1979. *Cupiennius salei* Keys. (Araneae) in the highlands of central Guatemala. Journal of Arachnology 7:255–263.
- Barth, F.G., E-A. Seyfarth, H. Bleckmann & W. Schüch. 1988. Spiders of the genus *Cupiennius* Simon 1891 (Araneae, Ctenidae). I. Range distribution, dwelling plants, and climatic characteristics of the habitats. Oecologia 77:187–193.
- Curio, E. 1976. The Ethology of Predation. Springer-Verlag, Berlin. 250 pp.
- Edmunds, M. 1974. Defence in Animals: A Survey of Anti-Predator Defences. Longman, New York. 357 pp.
- Elner, R.W. & R.N. Hughes. 1978. Energy maximization in the diet of the shore crab, *Carcinus maenas*. Journal of Animal Ecology 47:103–116.

- Eisner, T. 1970. Chemical defense against predation in arthropods. Pp. 157–217. *In* Chemical Ecology. (E. Sondheimer & J.B. Simeone, eds.). Academic Press, New York.
- Eisner, T., C. Rossini, A. González & M. Eisner. 2004. Chemical defense of an opilionid (*Acan-thopachylus aculeatus*). Journal of Experimental Biology 207:1313–1321.
- Foelix, R.F. 1996. Biology of Spiders. Second edition. Oxford University Press, New York. 330 pp.
- Gasnier, T.R. & H. Höfer. 2001. Patterns of abundance of four species of wandering spiders (Ctenidae, *Ctenus*) in a forest in central Amazonia. Journal of Arachnology 29:95–103.
- Gelperin, A. 1968. Feeding behaviour of the preying mantis: a learned modification. Nature 219: 399–400.
- Gnaspini, P. & J.A. Cavalheiro. 1998. Chemical and behavioral defenses of a Neotropical cavernicolous harvestman: *Goniosoma spelaeum* (Opiliones: Laniatores: Gonyleptidae). Journal of Arachnology 26:81–90.
- Höfer, H., A.D. Brescovit & T. Gasnier. 1994. The wandering spiders of the genus *Ctenus* (Ctenidae, Araneae) of Reserva Ducke, a rainforest in central Amazonia. Andrias 13:81–98.
- Krebs, J.R., J.T. Erichsen, M.I. Webber & E.L. Charnov. 1977. Optimal prey selection in the great tit *Parus major*. Animal Behaviour 25:30– 38.
- Machado G., P.C. Carrera, A.M. Pomini & A.J. Marsaioli. 2005. Chemical defense in harvestmen (Arachnida, Opiliones): do benzoquinone secretions deter invertebrate and vertebrate predators? Journal of Chemical Ecology 31:2519– 2539.
- Meire, P.M. & A. Ervynck. 1986. Are oystercatchers (*Haemoptopus ostralegus*) selecting the most profitable mussels (*Mytilus edulis*)? Animal Behaviour 34:1427–1435.
- Nentwig, W. 1986. Non-web building spiders: prey specialists or generalists? Oecologia 69:571–576.
- Salvestrini, F.M.D. & T.R. Gasnier. 2001. Differences in the activity of juveniles, females and males of two hunting spiders of the genus *Ctenus* (Araneae, Ctenidae): active males or inactive females? Journal of Arachnology 29:276–278.
- Van Loon, J.J.A. & M. Dicke. 2001. Sensory ecology of arthropods utilizing plant infochemicals. Pp. 253–270. *In* Ecology of Sensing (EG. Barth & A. Schmid, eds.). Springer Verlag, Berlin.
- Willemart, R.H. & G.E. Kaneto. 2004. On the natural history of the Neotropical spider *Enoploctenus cyclothorax* (Araneae, Ctenidae). Bulletin of the British Arachnological Society 13:53–59.
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