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Predation among armored arachnids: *Bothriurus bonariensis* (Scorpions, Bothriuridae) versus four species of harvestmen (Harvestmen, Gonyleptidae)

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ABSTRACT

Natural selection shapes prey-predator relationships and their behavioral adaptations, which seek to maximize capture success in the predator and avoidance in the prey. We tested the ability of adults of the scorpion *Bothriurus bonariensis* (Bothriuridae) to prey on synchronous and sympatric adults harvestmen of *Acanthopachylus aculeatus*, *Discocyrtus prospicuus*, *Parampheres bimaculatus* and *Pachyloides thorellii* (Gonyleptidae). In 72.5% of the cases *B. bonariensis* tried to prey on the harvestmen. The most successful captures occurred in the trials against *A. aculeatus* and *D. prospicuus*. In all the successful attacks the scorpions stung the prey between the chelicerae and consumed them, starting by the anterior portion of their bodies. The harvestmen used different defensive strategies such as fleeing before or after contact with the predator, exudating of chemical substances or staying still at the scorpion's touch. When scorpions contacted the chemical substances secreted by the harvestmen, they immediately rubbed the affected appendix against the substrate. However, exudating of chemical substances did not prevent, in any case, predation on the harvestmen. This is the first study showing the ability of scorpions to prey on different species of harvestmen, as well as the capture and defensive behaviors used by the predator and the prey.

1. Introduction

Among the processes of natural selection, one of the most interesting interspecific relationships is that between predator and prey, which drives the evolution of an "arms race" of offensive and defensive structures and behaviors that maximize success in each role (Dawkins and Krebs, 1979). Animals have a large defensive repertoire for predators that is displayed when the predator approaches the prey (prior to first contact) or when the prey is attacked (after first contact) (Edmunds, 1974; Redondo, 1994). Arthropods have several primary defense mechanisms to avoid detection by the predators, such as crypsis, mimicry or anachoresis (González et al., 2004; Pomini et al., 2010). Once the prey is detected, they can display secondary defensive behaviors such as standing still, simulating death (tanathosis), autotomizing appendices, fleeing, flying away, and even performing aggressive behaviors like holding with thorns or jaws, or exudating defensive secretions (Eisner et al., 1971; Cokendolpher, 1987; Cloudsley-Thompson, 1995; Eisner et al., 2005; Gnaspini and Hara, 2007; Pomini et al., 2010; Schaider et al., 2011). Exudating of chemical compounds is one of the most studied defensive behaviors and has appeared independently in many groups of vertebrates and invertebrates (Eisner, 1970; Blum, 1981; Eisner et al., 2005; McClintock and Baker 1997; Wood et al., 2002; Peters et al., 2009).

Harvestmen are excellent models to study defensive behavior as they can show both primary and secondary defenses against predators. They can remain unnoticed by performing crypsis or camouflaging themselves with debris. Harvestmen can also defend themselves by simulating death, pinching the offender with spines on their legs or other body parts, grasping the offender with chelicerae and pedipalp spines, or exudating defensive secretions (Pabst, 1953; Cokendolpher, 1987; Acosta et al., 1993; Martens, 1993; Gnaspini and Cavalheiro, 1998; González et al., 2004; Pereira et al., 2004; Machado et al., 2005; Gnaspini and Hara, 2007; Machado and Pomini 2008; Pomini et al., 2010; Schaider et al., 2011).

Harvestmen irritating chemical substances are secreted through two exocrine glands located in the anterior margins of the carapace,

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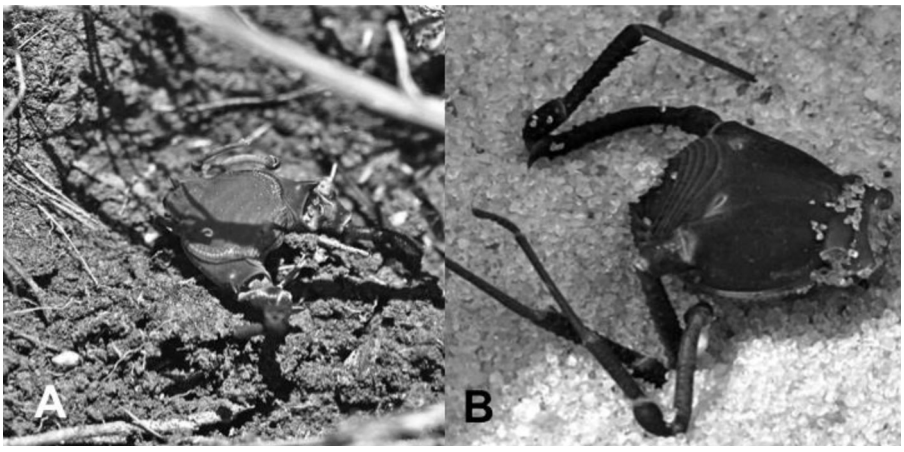

Fig. 1. (A) Remains of a male of *Acanthopachylus aculeatus* found under a rock in Piedras de Afilar. (B) Remains of a female of *Acanthopachylus aculeatus* after a succesfull attack by *Bothriurus bonariensis* under laboratory conditions.

near the second pair of legs, and opening to the outside through two pores located on the sides of the body between legs I and II, or on the back of the body (Shultz, 1990). The chemical composition of these secretions consists of a mixture of two substances: a colorless and odorless substance emerging from the mouth named enteric fluid, and another substance of strong odor named glandular substance (Eisner et al., 1977, 2004). The enteric substances move by capillary action along lateral channel above the coxae I–III until attain the ozoporo, where the glands are open to outside. These glands discharge a strong odor substance and which is mixed with the drop of enteric fluid (see Acosta et al., 1993 for more details). In Laniatores, and particularly in Gonyleptidae, this glandular secretion is mainly composed of benzoquinones and phenols and it can spread actively or passively (Eisner et al., 1978; Acosta et al., 1993; Gnaspini and Cavalheiro, 1998; Machado et al., 2000, 2005; Gnaspini and Hara, 2007; Machado and Pomini, 2008; Föttinger et al., 2010).

Despite these defenses, harvestmen have an extensive list of predators, including vertebrates (amphibians, birds, mammals and reptiles) and invertebrates (spiders and insects) (Cokendolpher and Mitov, 2007). Within arachnids, spiders are probably the most common predators of harvestmen, even those belonging to guilds as diverse as orb weavers, or soil and foliage runners (Cokendolpher and Mitov, 2007; Souza and Willemart, 2011; Carvalho et al., 2012; Dias and Willemart, 2013). In contrast, only Cloudsley-Thompson (1958) refers to one scorpion feeding on harvestman, but he does not report its specific name (see Cokendolpher and Mitov, 2007).

Scorpions are nocturnal hunters that do not depend of vision to capture prey. They gain information about their environment detecting vibrations propagated by the substrate and air displacement through sensory organs such as trichobothria on pedipalps, tarsal organs in the tarsus of the legs and pectines on the ventral area of the body (Abushama, 1964; Brownell and Farley, 1979; Brownell, 1988; McCormick and Polis, 1990; Mineo and Del Claro 2006).

We have observed the occurrence remainings of harvestmen (*Acanthopachylus aculeatus*, *Discocyrtus prospicuus* and *Parampheres bimaculatus*) in the vicinity of underground shelters of the black scorpion *Bothriurus bonariensis* (Koch, 1842) (Fig. 1). Also, the four species of harvestmen: *A. aculeatus* (Kirby, 1818), *P. bimaculatus* (Mello-Leitao, 1932), *Pachyloides thorellii* (Holmberg, 1878) and *D. prospicuus* (Holmberg, 1876) are synchronous and sympatric with the black scorpion *B. bonariensis*. The objective of this paper is to describe, the predatory behavior of *B. bonariensis* on those four species of harvestmen, quantifying the predatory success and reporting the defensive behaviors displayed by the harvestmen.

2. Material and methods

2.1. Study species

A. aculeatus, *P. bimaculatus*, *P. thorellii* and *D. prospicuus* occur in Southern South America. In Uruguay individuals of the four species of harvestmen are found in humid environments such as pastures (Capocasale, 2003; Capocasale and Gudynas, 1993; Toscano-Gadea and Simó, 2004). The period of activity of the four species coincides and occurs during spring and summer months (from October to March). Adult sizes are between 1 and 1.5 cm long, excluding locomotors appendages (Aisenberg et al., 2011). When *A. aculeatus* and *P. thorellii* are manipulated, they secrete an intense substance, composed by 1,4-benzoquinones (González et al., 2004). The chemical composition of the substance secreted by *D. prospicuus* is unknown. Instead, *P. bimaculatus* secretes a substance, which would be mainly composed by ketons. Unlike other species that open the repugnant glands in the anterior region of prosoma, *P. bimaculatus* has the opening of its glands on the surface of prosoma. These openings are located together with two elliptical orange spots that could play an aposematic role (González et al., 2004).

The black scorpion *B. bonariensis* occur in Southern South America (Fet et al., 2000; Ojanguren-Affilastro, 2005). In Uruguay, it is found in different environments: hilly areas, pastures, natural forests and woodlands with exotic vegetation, areas near the Rio de la Plata and even associated with human constructions (San Martín, 1961; San Martiín and Gambardella, 1967; Ojanguren-Affilastro, 2005; Toscano-Gadea, 2013). It has a size of between 5 and 7 cm long and, during night, feeds on a wide variety of insects and arachnids (Toscano-Gadea, unpublished data). Its surface activity occurs during the warm months (October–March) (Maury, 1973; Costa and Peírez-Miles, 1994; Toscano-Gadea, 2002).

2.2. Specimens collected and maintenance in the laboratory

Eighty specimens of *B. bonariensis* (40 males and 40 females) were collected at the hills and meadows of Piedras de Afilar, Canelones (34°46′06.31″S, 55°33′15.94″W) using blacklight flashlights, between November 2010 and February 2011. The scorpions were individually housed in Petri dishes of 8.5 cm diameter and 1.5 cm height, with sand as substrate and a cotton swab dipped in water. The specimens were fed once a week with larvae of *Tenebrio molitor* Linnaeus, 1758 (Coleoptera, Tenebrionidae) or juveniles of *Blaptica dubia* Serville, 1839 (Orteoptera, Blattellidae).

Eighty harvestmen (10 males and 10 females of each species) were collected by hand capture at three coastal locations of the Rio