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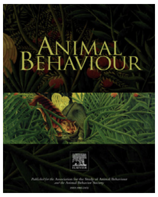

Delicate fangs, smart killing: the predation strategy of the recluse spider

Júlio M. G. Segovia [a, b, c], Kleber Del-Claro [a], Rodrigo Hirata Willemart [b, c, d, *]

[a] *Instituto de Biologia, Campus Umuarama, Uberlândia, MG, Brazil*
[b] *Laboratório de Ecologia Sensorial e Comportamento de Artrópodes (LESCA), Escola de Artes Ciências e Humanidades, Universidade de São Paulo, SP, Brazil*
[c] *Programa de Pós Graduação em Zoologia, Instituto de Biociências, Universidade de São Paulo, SP, Brazil*
[d] *Programa de Pós Graduação em Ecologia e Evolução, Universidade Federal de São Paulo, SP, Brazil*

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Prey consumption depends on the predator's ability to locate, capture and handle prey. We investigated these three steps in interactions between the delicate-bodied recluse spider *Loxosceles gaucho* (Araneae) and a heavy-bodied and armoured harvestman, *Mischonyx cuspidatus* (Opiliones). Although previous research suggested that the hard integument of such harvestmen protects them from being preyed upon by spiders larger than *Loxosceles*, indirect evidence suggested that *Loxosceles* spiders can subdue these prey. In the present study, we tested the following three hypotheses with regard to *L. gaucho*: (1) spiders use chemical cues left by prey to select foraging sites; (2) vibratory cues of prey are essential information in the predatory process; and (3) the spider's web sheet allows adequate handling of prey so vulnerable body regions of the prey can be bitten. To understand how a delicate predator can overcome the defences of a heavy-bodied and well-defended prey, we also quantitatively described the spider's behaviour. To test hypothesis 1, we compared the time spent in areas with harvestmen, crickets and no cues. For hypothesis 2, we compared latency to bite and number of bites in the presence or absence of vibratory information, and for hypothesis 3, we compared latency to detect prey, latency to capture prey and predation success. All three hypotheses were rejected. *Loxosceles gaucho* seems to be exceptional among spiders by not needing its web, indirect prey chemical cues, or prey's substrate borne vibrations to hunt the tested prey. What enables *L. gaucho* to prey upon *M. cuspidatus* is its unique hunting strategy, compared to previously studied spiders: it touches the prey with its tarsi possibly to locate weak parts of the prey's body, such as joints and distal parts of the legs, then it delivers several bites to these vulnerable areas. Our study is the first to document and describe how recluse spiders overcome the defences of an armoured harvestman.

Predator–prey interactions shape the behaviour and morphology of the interactants so that both prey defences and predatory strategies improve over evolutionary time in a process known as an ‘arms race’ (Dawkins & Krebs, 1979). From the predator's point of view, the predatory process encompasses the phases of searching for, capturing and handling prey (Davies, Krebs, & West, 2012). The search phase begins with the choice of a foraging site. Distinct pieces of information are used to assess the quality of a site, such as the presence of conspecifics (see Danchin, Giraldeau, Valone, & Wagner, 2004; Valone, 2007), environmental characteristics that potentially attract prey, the presence of prey or their cues, or physical characteristics that facilitate prey capture (Chien & Morse, 1998; Clark, Jackson, & Cutler, 2000; Hanna & Eason, 2013; Hopcraft, Sinclair, & Packer, 2005; Johnson, Revis, & Johnson, 2011).

After selecting a foraging site, predators detect prey using distinct sensory modalities. These include vision in frogs (González-Bernal, Brown, Cabrera-Guzmán, & Shine, 2011), perception of substrate-borne vibrations in scorpions (Mineo & Del-Claro, 2006), echolocation in bats (Schnitzler & Kalko, 2001), tactile sense in star-nosed moles and shrews (Anjum, Turni, Mulder, van der Burg, & Brecht, 2006; Catania & Remple, 2005), thermal sensitivity in snakes (Buning, 1983) and chemoreception in salamanders (Placyk & Graves, 2002), for example. In some cases, multiple sensory modalities are important for prey detection (Piep, Radespiel, Zimmermann, Schmidt, & Siemers, 2008). Features of

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* Correspondence: R. H. Willemart, Laboratório de Ecologia Sensorial e Comportamento de Artrópodes (LESCA), Escola de Artes Ciências e Humanidades, Universidade de São Paulo, SP, Brazil.

E-mail address: willemart@usp.br (R. H. Willemart).

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the microhabitat and prey behaviour directly influence the foraging behaviour and sensory modalities used by predators (e.g. Cunningham, Castro, & Potter, 2009; O'Rourke, Hall, Pitlik, & Fernández-Juricic, 2010; Van Buskirk & Nevitt, 2008).

After detecting prey, predators must capture and handle them, both of which involve use of distinct morphological structures and behaviours. For example, snakes use venom or constriction (Greene & Burghardt, 1978; Kardong, 1986), chameleons rapidly extend their sticky tongues (de Groot & Leuween, 2004; Herrel, Meyers, Aerts, & Nishikawa, 2000), insects may move over the prey and bite them quickly (De la Mora, Pérez-Lachaud, & Lachaud, 2008) or use raptorial legs to grasp prey (Betz & Mumm, 2001; Corrette, 1990).

The three phases of the predatory process, namely searching, capturing and handling, have seldom been studied collectively in spiders. Most spiders are polyphagous (Foelix, 2011; Nelson & Jackson, 2011) and their diet often includes arthropods in general. During the search phase, spiders use multiple cues to locate prey and, depending on the species, chemical cues can be particularly important (Jackson, Clark, & Harland, 2002; Persons & Rypstra, 2000; Persons & Uetz, 1996). During the capture phase, when the prey is close, substrate-borne vibrations play a fundamental role in prey capture by web spiders, wandering spiders and even by spiders that capture prey in aquatic environments (Barth, 2002; Bleckmann & Barth, 1984; Masters, 1984). Spiders use specific body structures (e.g. chelicerae, pedipalps or adhesive setae on the legs) and/or venom to capture and/or handle prey (Foelix, 2011; Rovner, 1980). A web is also often used (Coyle, 1986; Zschokke, Hénaut, Benjamin, & García-Ballinas, 2006).

Harvestmen are among the several species eaten by spiders and they show many kinds of defences such as cripsis, thanatosis, anachoresis, aposematism, mimicry, deimatic behaviour and fleeing (see Gnaspini & Hara, 2007). Chemical defence has been the most studied, with harvestmen releasing defensive secretions through glandular openings positioned laterodorsally on the body (Eisner, Rossini, González, & Eisner, 2004; Hara, Cavalheiro, Gnaspini, & Santos, 2005; Hara & Gnaspini, 2003; Machado & Pomini, 2008; Pomini, Machado, Pinto-da-Rocha, Macías-Ordóñez, & Marsaioli, 2010). Such chemicals are effective against some spiders (e.g. Machado, Carrera, Pomini, & Marsaioli, 2005), but they are not always used (Segovia, Del-Claro, & Willemart, in press). Instead, the thick cuticle of adult harvestman appears to be protective against some predatory spiders (Dias & Willemart, 2013; Souza & Willemart, 2011). A spider that cannot pierce the thick cuticle is left with only a few vulnerable spots to bite, such as the distal parts of legs, mouth and articulations (Souza & Willemart, 2011). When tested with heavy-bodied laniatorid harvestmen as prey, wandering spiders showed low capture rates despite their large size or their ability to spit venom (Carvalho, Souza, & Willemart, 2012; Dias & Willemart, 2013; Eisner et al., 2004; Souza & Willemart, 2011). Moreover, the large *Enoploctenus cyclothorax* did not feed on *Mischonyx cuspidatus* harvestman even after sharing a small terrarium with it for about 70 days and with no alternative food source (Willemart & Pellegatti-Franco, 2006). In contrast, we often find dead harvestmen on the horizontal web sheets of recluse spiders (*Loxosceles*) (J. M. G. Segovia & R. H. Willemart, personal observations; Fischer, Vasconcellos-Neto, & dos Santos Neto, 2006). Despite being well known for causing severe skin wounds and being of medical importance (Cardoso, França, Wen, Malaque, & Haddad, 2009), there are no detailed studies on how *Loxosceles* spiders hunt their prey. Because the body and chelicerae of these spiders are delicate, Carvalho et al. (2012) hypothesized that they use sheet webs to capture and immobilize harvestmen prey, allowing them to bite the vulnerable parts of the harvestman's body.

We examined distinct phases of prey capture during interactions between a recluse spider (*Loxosceles gaucho*) and a heavy-bodied harvestman (*Mischonyx cuspidatus*). We first hypothesized that *Loxosceles gaucho* uses chemical cues left by prey to select a foraging site. Then, we hypothesized that they rely on vibratory cues to detect prey, since recluse spiders have poor vision (Sandidge & Hopwood, 2005) and because vibratory cues provide important information for spiders (e.g. Barth, 2002). We also tested the hypothesis that the web sheet allows recluse spiders to handle their prey more easily so that vulnerable areas of the prey can be bitten (Carvalho et al., 2012). To understand how a delicate predator can overcome the defences of a heavy-bodied and well-defended prey that is rejected by much larger predators (Dias & Willemart, 2013; Souza & Willemart, 2011), we also quantitatively described the spider's behaviour.

METHODS

Study Species

The harvestmen *Mischonyx cuspidatus* (Roewer 1913) and spiders of the genus *Loxosceles* are active mainly at night (Fischer et al., 2006; Pereira, Elpino-Campos, Del-Claro, & Machado, 2004) and can be found under tree trunks, dead palm fronds and man-made structures, often under bricks (Fischer & Vasconcellos-Neto, 2005; Mestre & Pinto-da-Rocha, 2004). *Loxosceles* spiders feed on a wide variety of arthropods (Fischer et al., 2006), and the webs of these spiders are uneven and can often be found inside or near houses (Sandidge & Hopwood, 2005). However, *Loxosceles* spiders can also capture prey when wandering outside their webs (see Fischer et al., 2006; Vetter, 2008), but to our knowledge there is no detailed study on the time spent off the web or the frequency with which they leave their webs.

We collected *L. gaucho* in Mairiporã, São Paulo, Brazil (23°19′S, 46°35′W), from building material, between November 2012 and February 2013. We found individuals of *M. cuspidatus* on the same bricks where the spiders were collected, but not in enough quantity for the experiments. The harvestmen *M. cuspidatus* used in the experiments were therefore collected from under tree trunks at Parque Ecológico do Tietê, São Paulo, São Paulo (23°25′S, 46°28′W), between December 2012 and May 2013.

Laboratory Conditions

We maintained the animals in the laboratory under ambient temperature on a natural light:dark cycle, but with a weak red light (15 W) turned on 24 h per day, which allowed us to work at night without disturbing the animals. We maintained spiders and harvestmen individually in plastic containers (12 × 8 and 4 cm high, except in experiment 3; see below) with soil on the bottom. We provided water with a wet cotton ball only for harvestmen since high humidity appeared to be deleterious to the *Loxosceles* spiders. We fed the spiders either harvestman or crickets, according to the experiments, as described below, and we gave harvestmen moistened dog food once per week. The crickets (*Gryllus* sp.) were purchased from a commercial supplier. They were fed dry dog food and maintained under the same laboratory conditions as the spiders and harvestmen. The mean ± SD body sizes of animals used were as follows: spiders: 1.057 ± 0.15 cm ($N = 108$); harvestmen: 0.797 ± 0.07 cm ($N = 64$); crickets: 1.284 ± 0.17 cm ($N = 30$). We used crickets that were longer than the harvestmen because the harvestmen were wider than the crickets. The integument of the harvestmen (thickness of tibia cuticle: ~58 μm) is also thicker than that of the crickets used in this experiment (thickness of tibia cuticle: ~19 μm; Dias & Willemart, 2013).