

SHORT COMMUNICATION

Intense leg tapping behavior by the harvestman *Mischonyx cuspidatus* (Gonyleptidae): an undescribed defensive behavior in Opiliones?

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Abstract. We describe for the first time the behavior “Intense Leg Tapping (ILT)” being used in a prey-predator context between the Neotropical harvestman *Mischonyx cuspidatus* (Roewer 1913) and the syntopic spider *Ctenus ornatus* (Keyserling 1877). Previously, the harvestman’s repeated fast dorsoventral movements of legs II had only been described during conspecific male-male interactions. We suggest it has a defensive function.

Keywords: Ctenidae, defense, deimatic, harvestmen, spider

Prey species often produce signals toward predators according to the sensory modality these predators use. Several invertebrates and vertebrates use colors or body marks against visual diurnal predators (Eisner et al. 2005; Caro 2009; Stevens & Ruxton 2012); moths produce sounds against nocturnal predators that use echolocation to hunt, such as bats (Conner & Corcoran 2012), and squirrels increase the temperature of their tail specifically against predators sensitive to minimum temperature variation, such as vipers (Rundus et al. 2007). Such signals function either to warn the predator of a potentially dangerous defense or distastefulness (the case of aposematism) or to startle the predator (the case of deimatic behaviors), causing it to hesitate or give up attacking (Edmunds 1974).

Ctenid spiders are nocturnal hunters that feed on a variety of arthropods by quickly jumping onto them, biting and injecting venom (Höfer et al. 1994; Wullschlegel & Nentwig 2002). Though they may detect visual stimuli, eyes are not necessary to find prey: they rely almost exclusively on substrate and air borne vibrations and air displacement to catch prey detected by the very sensitive metatarsal organs and trichobothria on their legs (Barth 2002). Therefore, if a prey was to use any deimatic behavior or send warning signals to such spiders, one could expect it to use air displacements or vibrations.

Harvestmen are known to defend themselves in several ways. The list includes anachoresis, the use of chemical deterrents from repugnatorial glands, fleeing, feigning death, leg autotomy and retaliation (Gnaspini & Hara 2007). A heavy armature has also been shown to be effective (Souza & Willemart 2011; Dias & Willemart 2013) and based on their colorful body, some species have been suggested to be aposematic (Gnaspini & Hara 2007; Pomini et al. 2010). In addition to these, the harvestman *Eumesosoma roeweri* (Goodnight & Goodnight 1943) (Sclerosomatidae) has been shown to avoid chemicals from predators (Chelini et al. 2009). Herein we describe a putative new defensive behavior in the order Opiliones, namely the intense dorso-ventral movements of legs II (Intense Leg Tapping – ILT, sensu Willemart et al. 2009a) of *Mischonyx cuspidatus* (Roewer 1913) against a predator sensitive to air displacements and vibrations, the large wandering spider *Ctenus ornatus* (Keyserling 1877) (Ctenidae) (Fig. 1).

Individuals of the harvestman *M. cuspidatus* and the spider *C. ornatus* were collected at the Reserva da Cidade Universitária Armando Salles de Oliveira, São Paulo State (23°33’S, 46°43’W). They were maintained individually in plastic containers (12 × 8 × 4 cm height for the harvestmen and 20 cm (diameter) × 8 cm height

for spiders) with soil on the bottom and cotton rolls for humidity. The harvestmen were fed on wet dog food and the spiders on crickets. Temperature was ambient (20–25°C) and the light cycle was natural (approximately 12:12 light:dark cycle).

We made the behavioral observations from May to September 2009 (spiders: six subadult males and 36 adult females; harvestmen: 42 individuals, 23 adult males and 19 adult females) and again in January 2011 (spiders: 10 females, three adult males and two immature individuals; harvestmen: three adult females and 11 adult males) under dim light, between 1800 and 2300 h. All the spiders were starved for 25–30 days before the observations. Each individual spider and harvestman was used only once, and the sequence was determined in random order. The circular arena used for the tests (20 cm diameter × 8 cm height) had humid soil on the bottom. A spider was introduced into this arena 8 h before the trial to minimize stress, and the harvestman was introduced in a vial as far as possible from the spider, allowed to acclimate for 2 min and then released. We used a Sony Handycam DCR-TRV361 ‘nightshot’ (hand held to allow recording from better angles, only one observer) to record the behaviors related to the approach between the two animals, the physical interaction and the 10 s subsequent to the interaction to determine if the spider would start eating the prey. Results are presented as “mean ± S.D.”

We observed four female and eight male *M. cuspidatus* displaying ILT against adult females of *C. ornatus*, out of 56 harvestmen observed. Intense Leg Tapping consisted of very rapid dorso-ventral movements of legs II, with either one or both legs. Harvestmen performed one or several bouts (sensu Lehner 1998) of ILT. The total number of bouts, pooling across all individuals and single and double leg bouts, was 74, 43 pointing toward the spider and 31 not pointing toward the spider. Among harvestmen that displayed ILT, males displayed 1.67 ± 0.5 single leg bouts and 2.6 ± 2.2 double leg bouts per interaction with spiders. Females displayed 1.75 ± 0.95 single leg bouts and 1.25 ± 1.26 double leg bouts per interaction with spiders. There was no difference between males and females (Mann-Whitney test: single leg bouts: $U = 28.0$, $P = 0.938$, $n = 4$ and 9; double leg bouts: $U = 19.0$, $P = 0.283$, $n = 4$ and 8). The mean duration of bouts was 4.96 ± 0.57 s (min: 3.4; max: 6.3) (data combined for all 74 bouts). Six harvestmen did not displace while exhibiting ILT, four moved toward the spider and two moved in the opposite direction. Eight harvestmen made contact with the spider before displaying ILT (in four cases contact was established because the spider attacked the harvestmen) and the remaining four did not. The distance between the anterior portion of the prosoma of spiders and the tip of the closest

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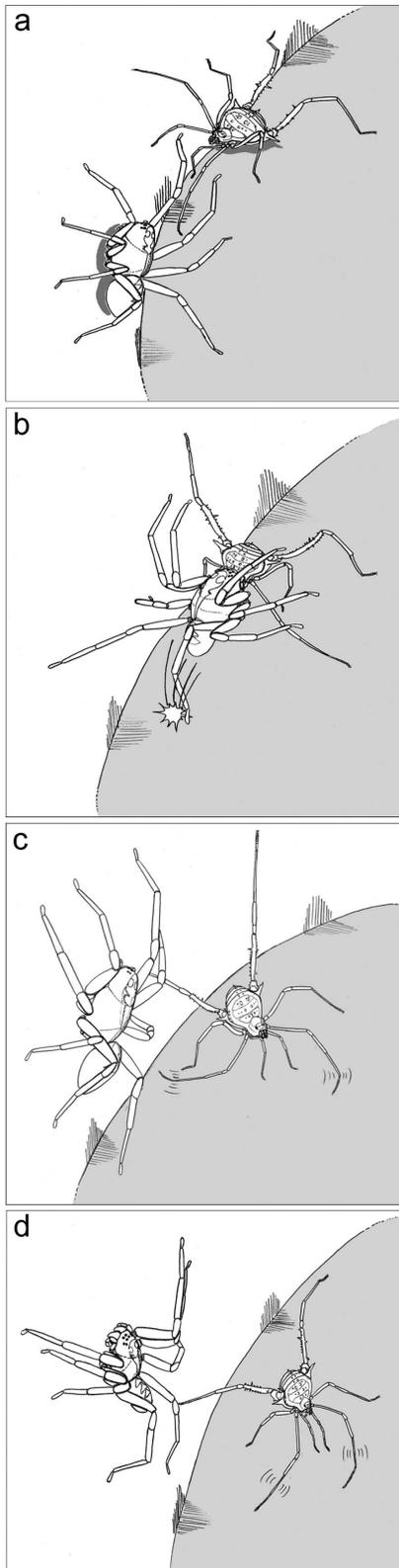


Figure 1.—a) The harvestman *Mischnonyx cuspidatus* touches the spider *Ctenus ornatus* with its leg II; b) the spider jumps onto the harvestman; c) the spider retreats and the harvestman starts displaying intense leg-tapping (ILT); d) the spider walks away.

leg of the harvestmen when ILT started was 4.4 ± 2.3 cm (max: 9.3, min: 1.8 cm, $n = 12$). In six cases, the spider did not move after the harvestman started displaying ILT. Five spiders moved in the opposite direction and one spider attacked.

Intense Leg Tapping is performed during male-male fights in the species *Neosadocus maximus* Giltay 1928 (Gonyleptidae) (Willemart et al. 2009a). The function of the behavior in that context remains unknown, but it was clear that the males only started ILT when fighting with conspecifics. Now that we have observed the same behavior by harvestmen in a predator-prey interaction, a very different context, we suggest that ILT is also a defensive behavior. We propose two main pieces of evidence. First, we have accumulated approximately 340 hours of behavioral observations that were taped in distinct contexts (resting, walking, interacting with conspecifics of both sexes, interacting with heterospecifics, foraging, etc.), of several harvestmen species (at least 13), in addition to field observations since 1999 that were not taped (R.H. Willemart and members of our laboratory, personal observations). Intense leg tapping had never been observed except in the context of male-male fighting and after making contact with a predator (see Willemart et al. 2009a; this paper). Second, the sensory modality exploited by the harvestman when displaying ILT is exactly what these spiders use when hunting, namely air displacement and vibrations (Barth 2002 and references therein). It could therefore be analogous to animals that use color, sounds or variation in body heat as a deimatic behavior or when signaling to predators that use each of these specific sensory modalities to hunt (Stevens 2007; Rundus et al. 2007; Ruxton 2009).

In almost half of the bouts in which ILT was observed, the behavior was not directed toward the spider. We believe this reflects the limited sensory abilities of the harvestmen and its inability to accurately detect nearby arthropods (Willemart et al. 2009b). We unfortunately do not have solid data on how the predator is affected by ILT. This is also the case for several mechanisms that have been considered to be defensive in harvestmen, such as nipping behavior, pinching with chelicerae and pedipalps, tanathosis and aposematism (Gnaspini & Hara 2007 and references therein). The fact that ILT has also been observed in conspecific fights is not evidence against the defensive hypothesis. Deer, antelope, and other mammals with horns or antlers use these weapons in male-male fights and for defense (Andersson 1994). Since both sexes of *M. cuspidatus* have been observed performing ILT, ILT in the sexual context (only males have been observed doing it) could be an exaptation (sensu Gould & Vrba 1982) of ILT in the defensive context. This would be more parsimonious than to believe that it first appeared in a sexual context among males, after which they also started using it in a defensive context, after which it then appeared again in females for defensive purposes.

An alternative hypothesis could be that these movements have a sensory function and that harvestmen are actually trying to gain information about the predator. Based on previous studies on the sensory biology of harvestmen (e.g., Willemart & Chelini 2007; Willemart et al. 2009b), this would be very unusual since laniatorid harvestmen use slow waving movements of legs I and II in the air or gently tap the substrate when stimuli are provided. These are very different from ILT.

Another alternative hypothesis is that ILT against predators is a displaced, out of context behavior with its origin in male-male fights, but that females also exhibit this behavior. Further studies with observations of ILT in multiple contexts would weaken the defensive hypothesis and maybe strengthen the “displaced behavior” hypothesis.

We have documented that ILT occurs in the context of prey-predator interaction. The defensive hypothesis could be further tested by examining exactly what stimuli trigger it or how it affects their predators, but alternative hypotheses should not be discarded at this point.

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