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REVIEW

Staying alive: how harvesters avoid predation

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Abstract. Harvester species exhibit a diverse array of defenses against predators. In this article, we briefly cover chemical defenses, coloration patterns, autotomy, aggregations, freezing behavior, bobbing, body vibration, and the production of sounds that might be used to avoid predators' attacks. Those defenses are not present in all harvester species and may not deter all kinds of predators. We discuss how prey-predator interaction may shape the evolution of defenses. Here we focus on studies that have been done after 2007, and we aim to give a general idea of the knowledge about prey-predator interactions in Opiliones to date, especially to the general public.

Keywords: Opiliones, arachnids, predation avoidance, harvestmen

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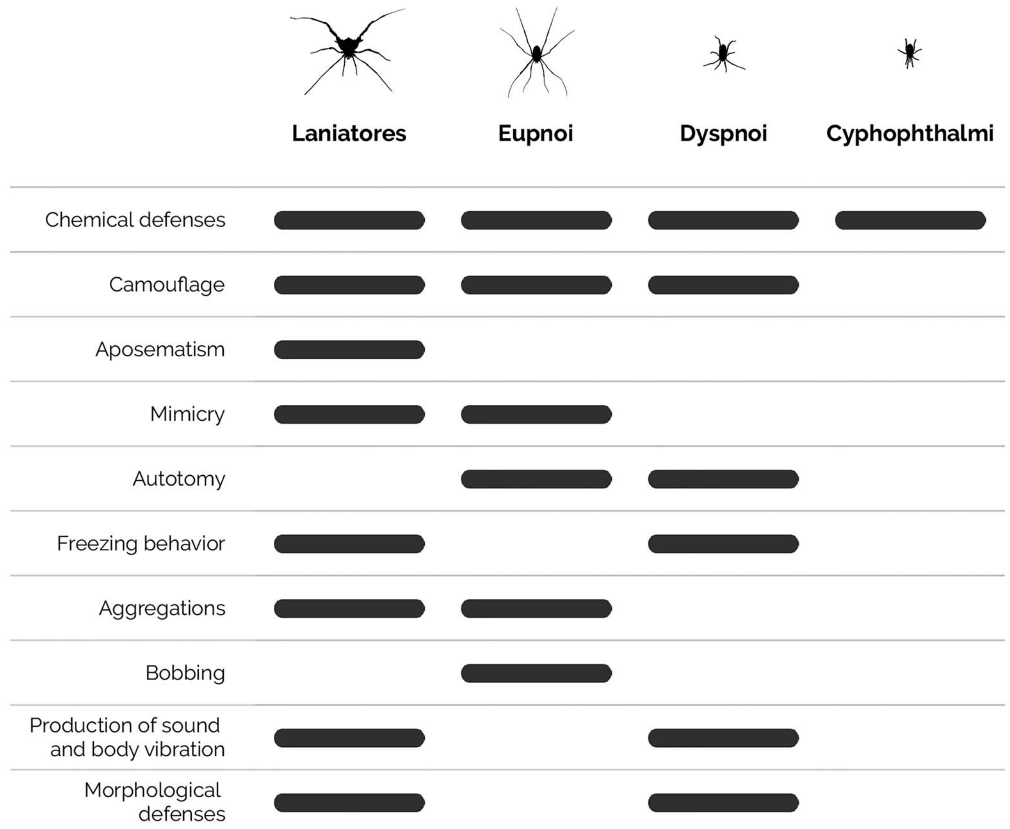
Predation is a strong selective pressure, and lacking adequate mechanisms to withstand it may mean death. Therefore, a range of defensive strategies is expected to evolve, obviously limited by constraints related to the morphological and physiological characteristics of prey. Harvesters not only exhibit great morphological variation but are also attacked by a diverse array of predators, making them an interesting group for studies on prey-predator interactions. We will discuss the diversity of defenses (Fig. 1) that these animals have developed and present experiments that demonstrate their effectiveness. We will give examples of predators such as ants, spiders, whip spiders, scorpions, flatworms, onychophorans, toads, lizards, opossums, and bears. Because the types of defenses vary among main groups within the order Opiliones, we identify the suborder when appropriate (Cyphophthalmi, Dyspnoi, Eupnoi, and Laniatores). This review certainly does not exhaust the subject but is intended to give a general idea of where researchers worldwide are in the knowledge of prey-predator interactions in Opiliones. Here we will not focus on studies that have been done before 2007, as there are excellent literature reviews (Cokendolpher & Mitov 2007; Gnaspini & Hara 2007). Many of the defenses mentioned here are also common to other arachnids, which were reviewed by Pékar & Raspotnig (2022).

CHEMICAL DEFENSES

Chemical defense is possibly the most diverse way of avoiding predation (Ruxton et al. 2004). This may be related to the fact that chemical perception, through olfaction or gustation, is present in most animal taxa, including predators (Stevens 2013). Unlike other arachnids such as spiders and scorpions, harvesters lack venom glands but produce defensive secretions, generally referred to as irritants, from a pair of scent glands (Fig. 2; Gnaspini & Hara 2007).

Emission of chemicals.—In general, harvesters first emit an aqueous fluid through the mouth, known as enteric fluid (mainly water; Gnaspini & Cavalheiro 1998). This liquid travels through external body channels by capillarity and reaches the opening of the glands, called the ozopore. Here the chemical secretion is emitted in liquid form and blends with that aqueous fluid (Hara & Gnaspini 2003; Gnaspini & Hara 2007). In Laniatores, three main discharge patterns have been observed so far (Fig. 2; Hara & Gnaspini 2003; see also Pagoti et al. 2019 for harvesters that apply chemicals on the aggressor with their legs): (a) emission of a droplet on each side of the body that does not spread along the body or emission of volatiles, (b) spread of the chemicals through the body in different patterns, (c) emission in a directional jet. In Dyspnoi, the surrounding structure of the glands' opening is different from other groups of harvesters, at least for the species studied so far (Schaider & Raspotnig 2009; Schaider et al. 2011; Raspotnig et al. 2014). In this suborder, the ozopore is inside a cavity; consequently, the types of emission may also be different (Schaider & Raspotnig 2009). Some species are very resistant to emitting it, suggesting that in these cases, the chemical secretion may have other functions than deterring predators (Schaider & Raspotnig 2009) or that it is very costly (see below). In *Paranemastoma quadripunctatum* (Perty, 1833), the enteric fluid is believed to be sucked into the gland reservoir before the diluted secretion is emitted through the ozopore (Schaider et al. 2011). Another atypical example of secretion discharge was found in the species *Trogulus tricarinatus* (Linnaeus, 1767), which releases an unknown compound in solid form (Schaider & Raspotnig 2009).

Diversity of chemicals among species.—The class of chemical defenses seems to be tightly associated with harvesters taxa (Raspotnig 2012; Raspotnig et al. 2017). Therefore, general trends may be observed for each suborder. In Laniatores, the main classes are benzoquinones, phenols, ketones, pyrans, alkaloids, and terpenes (see Caetano & Machado 2013; Raspotnig et al. 2015). Naphthoquinones, benzoquinones, alcohols, ethyl-ketone, and lactones characterize the chemical defenses of Eupnoi (Raspotnig et al. 2020), while naphthoquinones and anthraquinones are the defensive compounds of Dyspnoi (Raspotnig et al. 2014). Cyphophthalmi mainly produces naphthoquinones and methyl-ketones (Raspotnig 2012; Schaider et al. 2018). Note that, although the classes of chemical compounds seem more diverse for Laniatores (Fig. 3, Supplemental File S1, online at https://doi.org/10.1636/JoA-S-22-054.s1), this might be a biased view because this is the most studied group so far (Fig. 4). Two previous reviews describe in detail the chemicals produced by each species (Gnaspini & Hara 2007; Raspotnig 2012).



	Laniatores	Eupnoi	Dyspnoi	Cyphophthalmi
Chemical defenses	▬	▬	▬	▬
Camouflage	▬	▬	▬	
Aposematism	▬			
Mimicry	▬	▬		
Autotomy		▬	▬	
Freezing behavior	▬		▬	
Aggregations	▬	▬		
Bobbing		▬		
Production of sound and body vibration	▬		▬	
Morphological defenses	▬		▬	

Figure 1.—Diversity of defenses against predators present in different suborders of harvesters. The bars indicate the presence of the defense in each group.

Production of chemicals.—Among the classes of chemical compounds produced by Gonyleptidae, three of them – benzoquinones, phenols, and ketones – share a similar pathway of synthesis. An enzyme called polyketide synthase (PKS), involved in this process, is not produced by these arachnids, suggesting that an association with bacteria that produce PKS might exist (Pankewitz & Hilker 2008; Rocha et al. 2013a, b).

Costs of chemical defenses.—The effectiveness of chemical defenses in arthropods (Roth & Eisner 1962; Pasteels et al. 1983; Zvereva & Kozlov 2016) is widely acknowledged, but they also come at a cost, including the resources required for producing and storing the secretions (Ruxton et al. 2004). Although few studies have examined the costs incurred by harvesters, they provide evidence that chemical defense is indeed costly for these arachnids. For example, *Camarana flavipalpi* Soares, 1945 only emits chemicals when subjected to high levels of disturbance. Reluctance in emitting chemicals is widespread but varies among species and the aggressor (see discussion below). Additionally, a

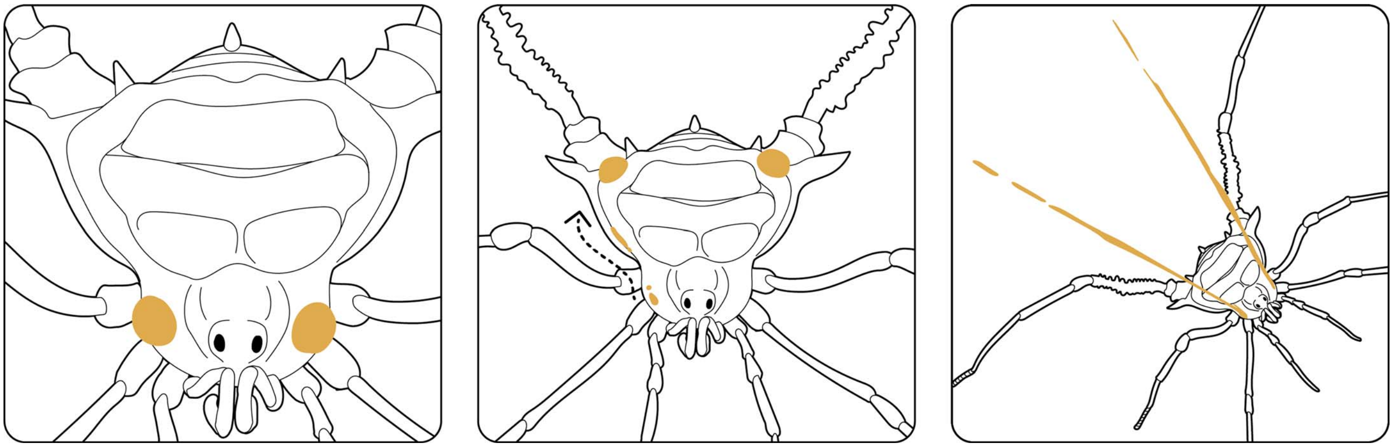


Figure 2.—Patterns of chemical defense secretion in Laniatores. From the left to the right: emission in a droplet through the ozopore (gland opening), emission flows in the lateral channels, (the direction is represented by an arrow), and emission in a fine jet. The chemical defense is represented in yellow, but not all chemicals are yellow. Illustrated by Vítor Marques de Faria.

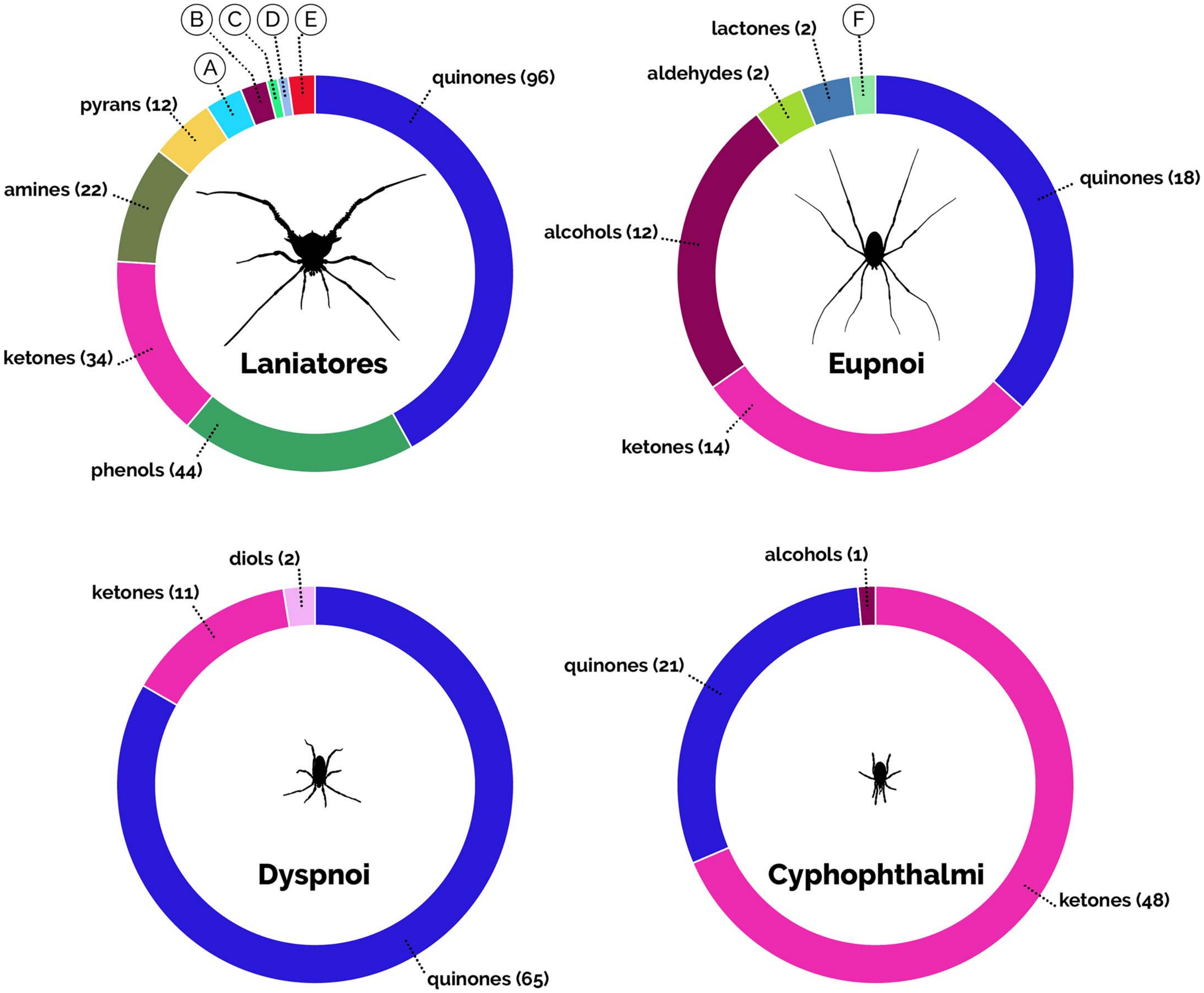


Figure 3.—Diversity of chemical defenses categories in the four suborders of harvesters, identified as of 2021; data collected from PheroBase. The size of each subsection represents absolute numbers of how many substances belong to each category.

study of *Magnispina neptunus* Mendes, 2011 found that the production of benzoquinones is condition-dependent, requiring a good nutritional state to produce a large amount of highly concentrated chemical defense (Nazareth et al. 2016). The chemical defense of *Acutisoma longipes* Roewer, 1913 females carrying eggs is less effective against ants and spiders than the defense of females without eggs, suggesting a trade-off between investment in reproduction and defense (Nazareth & Machado 2015).

Effectiveness of the chemicals against predators.—The mere presence of a chemical compound in a harvester's secretion is not enough evidence that it is a defensive mechanism against predators. Therefore, experiments that assess the predators' response to the compound are necessary. Some of those studies were reported in a review in 2007, and they have shown that harvesters' secretion is effective against ants, spiders, frogs, lizards, and hens but not against opossums (Figs. 5, 6; Gnaspini & Hara 2007). However, it is important to ponder that the effectiveness depends on both the harvester species and the predator species. Several studies with spiders have produced conflicting results, possibly due to differences in methods used (e.g., Machado et al. 2005; Souza & Willemart 2011). There are various reasons why predators might still consume chemically defended prey. Some predators might not find the chemicals distasteful, while for others, the nutritional value of the prey might outweigh the cost of consuming the chemicals (Barnett et al. 2012; Skelhorn et al. 2016). The predator's ability to convert the chemical secretion into its defense mechanism (Saporito et al. 2012; Wink 2019) might also play a role, although this has not been observed in animals that consume harvesters. Additionally, in low temperatures or when other prey options are nutritionally poor, predators may choose to consume chemically defended prey (Skelhorn et al. 2016; Marples et al. 2018).

Compounds with medical interest.—The alkaloid anabaseine, found in the endemic species *Holoscotolemon lessiniense* Martens, 1978 from the southern Alps, has the potential in treating cognitive loss caused by human diseases, as discussed in Raspotnig et al. (2011).

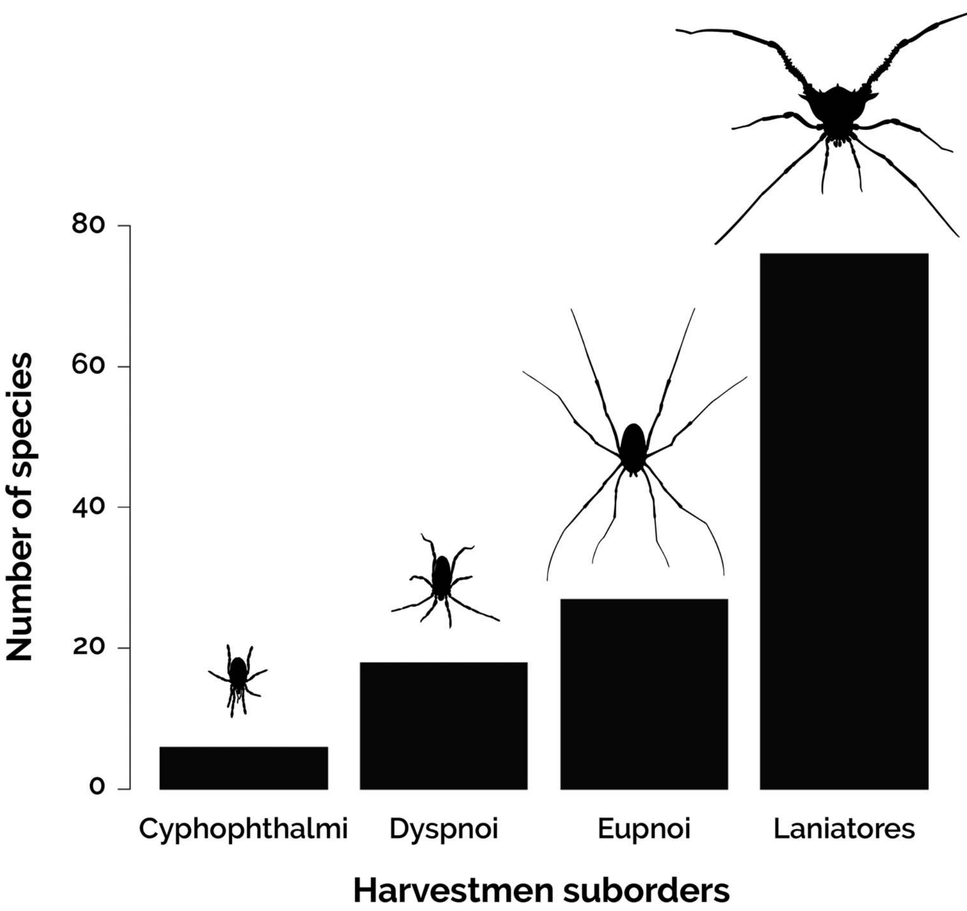


Figure 4.—Number of species whose compounds from chemical defenses were identified, from each harvester's suborder until the present time. Harvesters illustrations by Vítor Marques.

COLORATION

The coloration of an animal's body can serve various purposes, such as helping them find food or mates, or protecting them from predators (Cuthill et al. 2017). Among these, three strategies are commonly observed and studied. The first is camouflage, where the body coloration of an animal blends with the background to avoid detection by predators (Stevens & Merilaita 2009a; Merilaita et al. 2017). The background may include green or dry leaves, twigs, litter, or rocks. The second strategy is aposematism, where animals use bright colors such as red, yellow, and blue to warn predators of their toxic or distasteful nature (Mappes et al. 2005; Stevens & Ruxton 2012; Skelhorn et al. 2016). The third strategy is mimicry, where non-toxic animals imitate the coloration of toxic prey to deter predators from attacking them (Ruxton et al. 2004).

Camouflage.—Camouflage can take on different forms to conceal prey. Some species of harvesters, such as *Phalangium morio* Fabricius, 1779, *Phalangium opilio* (Linnaeus, 1758), and *Lacinius ephippiatus* (Koch, 1835), present an anteroposterior stripe on their dorsum that contrasts with the rest of their body. Similarly, *Graphinotus ornatus* Koch, 1839 has green edges on its carapace, which can create confusion about the body's boundaries (Fig. 7). These patterns of coloration align with the concept of disruptive coloration, which suggests that species with patches of contrasting colors are harder to detect because they break the body silhouette. Thus, the color patches may be visible to a predator but not perceived as part of the whole body of prey (Stevens & Merilaita 2009b). Unlike other forms of camouflage, disruptive coloration does not rely solely on background color for prey to remain undetected (Cuthill et al. 2005; Schaefer & Stobbe 2006). Although many harvester species are brownish—at least to the human eye—and appear camouflaged, their coloration only works if they inhabit habitats with similar colors, such as tree barks, dry leaves, litter, and rocks. Another type of camouflage seen in harvesters is soil crypsis (see references in Porto & Pérez-González 2020), in which glandular secretions on the external parts of the body glue soil particles to the body and conceal the organism. This has evolved independently several times in the group and is absent only in Cyphophthalmi. Camouflage may also be conferred by association with cyanobacteria; this was suggested by an observation of cyanobacteria in the dorsum of *Prionostemma* sp., in which the green coloration blends with the background covered by moss (Proud et al. 2012, see also Machado & Vital 2001).

Aposematism.—Although red or yellow coloration is uncommon in harvesters, *Leiobunum roseum* Koch, 1839 and *L. limbatum* Koch, 1861 are notable exceptions. These adults exhibit color patterns distinct from other species from the same genus, with light red and light orange patches, respectively. Such bright colors may serve as warning signals, as seen in other arthropods such as ladybugs (Mappes et al. 2005), indicating to predators that the species is chemically

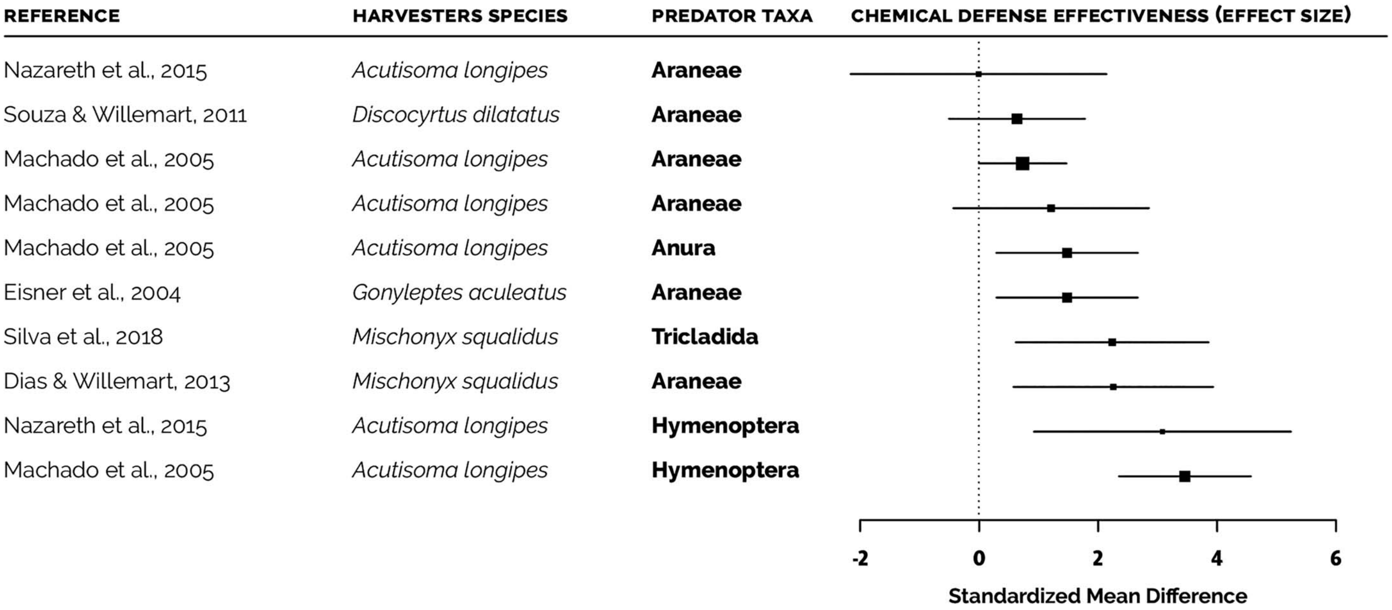


Figure 5.—Effect sizes computed as Standardized mean differences computed from studies that conducted controlled behavioral experiments to evaluate the effectiveness of chemical defenses of harvesters from the family Gonyleptidae against predators. Citations of each study are in the first column (from the left), harvesters' species in the second column, and predators' order in the third column. The effect sizes are equivalent to the difference of survival between the treatment with chemical defense and the control without chemical defense.

defended. Bright colors can help predators learn and remember unpleasant prey, distinguishing them from non-defended prey (Stevens & Ruxton 2012). Moreover, *L. roseum* and *L. limbatum* are typically found resting on exposed, gray rocky walls (C. Komposch, personal observation), which contrasts with what one would expect from non-defended animals. In fact, they are distasteful, at least to human taste buds (C. Komposch, personal observation).

Mimicry.—González et al. (2004) observed that the orange-colored spots in *Parampheres ronae* (Mello-Leitão, 1927) were very similar to yellowish quinolinic droplets that other species discharge. They suggested that these bright spots on *P. ronae* could be a form of mimicry, imitating the appearance of quinone-secreting species that predators find unappetizing (González et al. 2004), which repels predators. In this way, predators would avoid any prey looking like the one they learned to be distasteful. Interestingly, *P. ronae* is not the only species to exhibit yellowish spots near the secretion gland opening; *Paranemastoma quadripunctatum* and *Gonyleptellus cancellatus* (Roewer, 1917; see Fig. 8) also display a similar coloration pattern.

Predators' diversity of color vision systems.—Color vision relies on photoreceptors in the eye that respond to different light frequencies (Kelber et al. 2003; Jacobs 2012; Baden & Osorio 2019). There are four main ranges of frequency to which photoreceptors are sensitive: ultraviolet (UV), blue (B), green (G), and red (R). While some animals have four types of photoreceptors, this is not always the case (Kelber et al. 2003; Jacobs 2012; Baden & Osorio 2019). Among harvesters' predators, birds and reptiles typically have all four types of photoreceptors, while frogs and toads may have up to three types (B, G, and R) plus two others that are more active in low light conditions (B and G; Yovanovich et al. 2017). The opossum *Didelphis aurita* (Wied-Neuwied, 1826) has two types (UV and G; Hunt et al. 2009), insects (van der Kooi et al. 2021) and the spider *Cupiennius salei* (Keyserling, 1877) (Trechaleidae) (Walla et al. 1996) have three types of receptors (UV, B, and G; see Fig. 9). In addition to differences in sensitivity, other anatomical features can affect color perception, such as colored oil droplets, which act as spectral filters, found in birds, reptiles, and amphibians (Baden & Osorio 2019). Understanding the nuances of color vision across species is critical for comprehending animal coloration and reducing human biases in color perception. However, we currently lack quantitative data on harvesters' colors and predator vision, making it challenging to make predictions. Despite this, the striking colors of harvesters make them an exciting group to study the role of coloration in defense.

AUTOTOMY

When grabbed by a predator, species of the suborder Eupnoi often drop one of their legs and flee (Fig. 10). This strategy, known as autotomy (see Roth & Roth 1984 for discussion on autotomy *vs*. autospasy), increases the prey's chances of survival by freeing it from the predator and distracting the predator with the detached leg's movements (Emberts et al. 2019). Autotomy is common in the family Sclerosomatidae, and from sampling in five species, more than a quarter of individuals found had at least one leg missing (Houghton et al. 2011; Escalante et al. 2013, 2020a, b). Although losing a leg seems harsh, especially considering that a new leg does not grow back, harvesters cope well with the loss. For instance, *Prionostemma* Roewer, 1912 can recover velocity after two days even when losing three legs (Escalante et al. 2020a); *Nelima paessleri* (Roewer 1910) can maintain the oxygen level after losing one leg (Escalante et al. 2020b); and *Holmbergiana weyenberghii* (Holmberg, 1876) can still find food at the same velocity even after leg loss (Escalante et al. 2013). However, there are costs associated with autotomy. When the number of legs lost increases to three in *N. paessleri*,

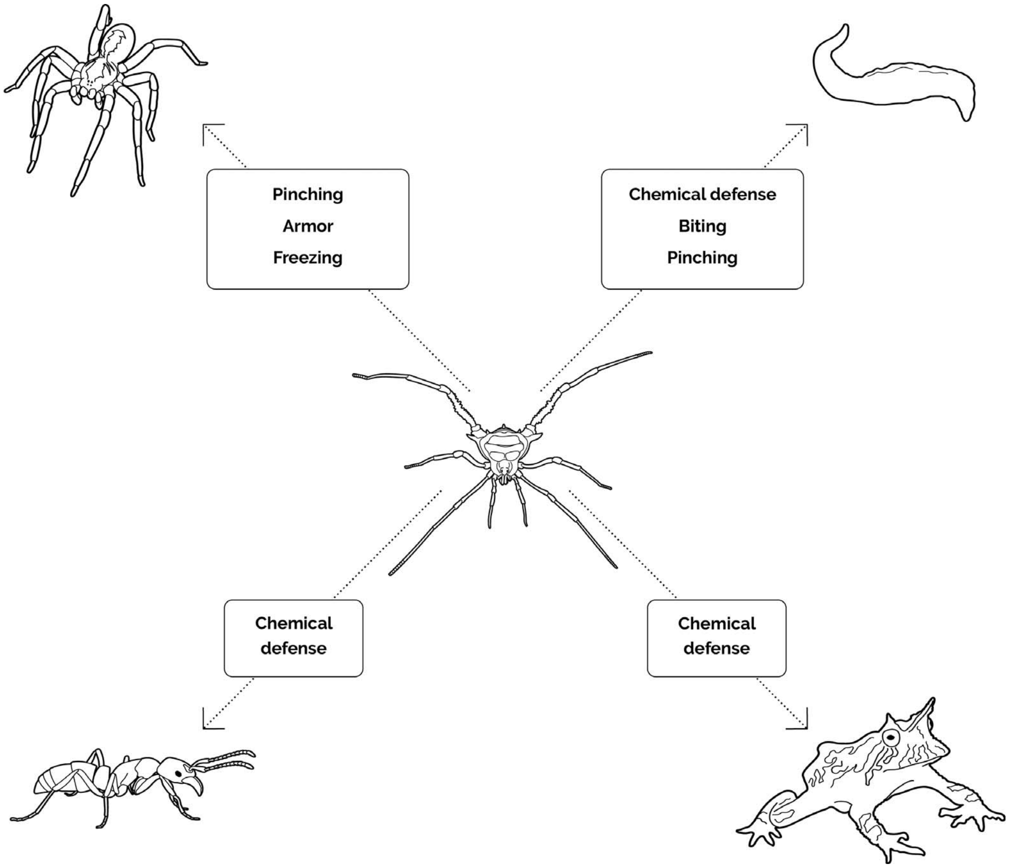


Figure 6.—Representation of some predators to which harvesters' defenses have been demonstrated to be effective. The type of defense that is effective for each predator is in the boxes. Predators from the upper right, clockwise: flatworm (*Cephaloflexa bergi*), toad (*Proceratophrys boiei*), ant (*Pachycondyla striata*) and spider (*Ctenus ornatus*). The effectiveness of chemical defenses is usually tested in the absence of the harvester. Illustrated by Vítor Marques de Faria.

the consumption of oxygen also increases, and the ability to walk continuously is reduced (Escalante et al. 2020b). The cost of a reduced walking speed is consistent among different species when individuals have autotomized legs (Guffey 1999; Houghton et al. 2011; Escalante et al. 2013, 2020a; Domínguez et al. 2016; Townsend et al. 2017). Climbing speed may also be affected by leg loss: *Leiobunum formosum* (Wood, 1868) and *L. politum* Weed, 1889 on vegetation occupy lower areas when compared to their counterparts with all eight legs (Houghton et al. 2011). Finally, foraging may also be affected by missing legs (Guffey 1999). According to anecdotal observations of neopilionid species, it appears that forest-dwelling species are more likely to autotomize their legs than their counterparts in caves. This observation could potentially indicate a lower level of predation pressure in cave-dwelling species (Powell et al. 2021).

FREEZING BEHAVIOR

In the presence of a threat, some species of harvesters may adopt a motionless posture with legs extended or retracted, which seems to be a common behavior (Fig. 11; Gnaspini & Hara 2007). Freezing has been observed in some gonyleptids sharing an arena with the scorpion *Bothriurus bonariensis* (C. L. Koch, 1842) (Albín & Toscano-Gadea 2015), in the presence of onychophorans, spiders, and under human manipulation (Machado & Pomini 2008; Pomini et al. 2010; Cook et al. 2013). Although not common in Eupnoi, freezing was recently reported in neopilionid species (Powell et al. 2021). Freezing helps prey to not be detected by predators but imposes foraging costs (Chelini et al. 2009). Some factors may influence the frequency of freezing; males of *Mischonyx squalidus* Bertkau, 1880 freeze less often than females do, maybe because they can rely on other defenses such as using spines that are absent in females (Segovia et al. 2019a). Individuals in this species also freeze more frequently during the day than at night, likely due to the higher chances of being detected in the daytime (Segovia et al. 2019b).

AGGREGATIONS

Harvesters can form aggregations of varying size and density, ranging from small and sparse to large and dense (Machado & Macías-Ordóñez 2007). Those groups can be found in hidden and dim areas (Machado 2002; Chelini et al. 2012), or exposed, depending on the species (Willemart & Gnaspini 2004; Machado & Macías-Ordóñez 2007; Grether et al. 2014b). The groups may even be composed of more than one species (Machado & Vasconcelos 1998; Chelini et al. 2012; Escalante et al. 2022). Harvesters may rely more on the chemicals of other individuals of the same species than on environmental cues to find an aggregation site, and these sites can be maintained for years (Grether

Figure 7.—*Graphinotus ornatus* (Gonyleptidae), Brazilian fauna. An example of possible disruptive coloration in which it may be hard to tell where the edges of the carapace actually are.

et al. 2014a, b). Advantages of aggregating include (a) increasing the intensity of the chemical defense odor by summing the secretion emitted by many individuals; (b) the possibility to flee rapidly due to efficient alarm communication (see Machado et al. 2002 for discussion of alarm pheromones); (c) reducing the chances of being found by a predator, because the occurrence frequency of aggregation is lower than the occurrence of many individuals separately (although aggregations are more easily spotted); and (d) and the lower risk of an individual being captured in a group due to dilution/confusion effects (Machado & Macías-Ordóñez 2007; Escalante et al. 2022). In aggregations with multiple species those benefits might vary for the species involved, influenced by their morphological and behavioral traits (Escalante et al. 2022). Areas chosen for aggregation are not random; humidity and low light may be important (Machado & Macías-Ordóñez 2007; Chelini et al. 2011), as may the physical characteristics of the substrate. For instance, *Prionostemma* sp. aggregates in trees with spines, and when these spines are removed, they move to another tree with spines if available (Donaldson & Grether 2007). The spines may deter lizards, which were observed once consuming a harvester in a tree with no spines (Donaldson & Grether 2007). However, aggregations may not deter large carnivores, as evidenced by the presence of harvesters in bear scats. Two out of 180 bear scats had 62 and 123 individuals of *Leiobunum* Koch, 1839 (Jones et al. 2016). These numbers suggest these harvesters were aggregated. Some possible costs of aggregation are (a) conspicuousness reinforcement, (b) greater resource competition, and (c) higher chances of infection by pathogens and parasites (Escalante et al. 2022). However, for *Prionostemma* sp. mite occurrence was equal for solitary and aggregated individuals (Escalante et al. 2022).

BOBBING

Some Eupnoi species rapidly move their body up and down upon disturbance, a behavior known as bobbing (Fig. 12; Gnaspini & Hara 2007). Researchers have hypothesized that this might be a defensive behavior, misleading predators about harvesters' body location, or a potential alarm communication because once some individuals start bobbing in an aggregation, other individuals disperse (Donaldson & Grether 2007; Gnaspini & Hara 2007). Bobbing was observed more frequently in the presence of a spider than in the presence of whip spiders or onychophorans (Cook et al. 2013). Harvesters also display this movement upon human disturbance (Donaldson & Grether 2007; Escalante et al. 2013; Grether et al. 2014a). However, there is no evidence to support the effectiveness of bobbing in deterring predators.

PRODUCTION OF SOUND AND BODY VIBRATION

Gnaspini & Hara (2007) have reviewed the literature on the stridulatory apparatus, which refers to body parts that produce sounds when scraped against each other. These have been described in Dyspnoi and Laniatores and involve mainly chelicerae, pedipalps, and legs. Although some harvesters have been seen vibrating when manipulated (e.g., Pomini et al. 2010; Townsend et al. 2019), the efficiency of this mechanism has yet to be demonstrated.

DEFENSIVE STRATEGIES DO NOT PROTECT AGAINST ALL PREDATORS

Historically, part of the literature on prey defenses seems to imply that all the defensive mechanisms of a particular species are functional against predators in general. However, prey often face

Figure 8.—*Gonyleptellus cancellatus* (Gonyleptidae), Brazilian fauna. Note the yellow spots next to the ozopore.

multiple predators with very different predatory strategies. Therefore, it is expected that several defensive strategies occur, but they should not necessarily protect against all or most predators. Distinct selective pressures are expected to be involved in the maintenance of distinct defensive mechanisms, and harvesters are interesting animals to study the subject because of their wide defensive repertoire.

A set of studies with Brazilian armored harvesters (suborder Laniatores) and some of their predators nicely illustrates this

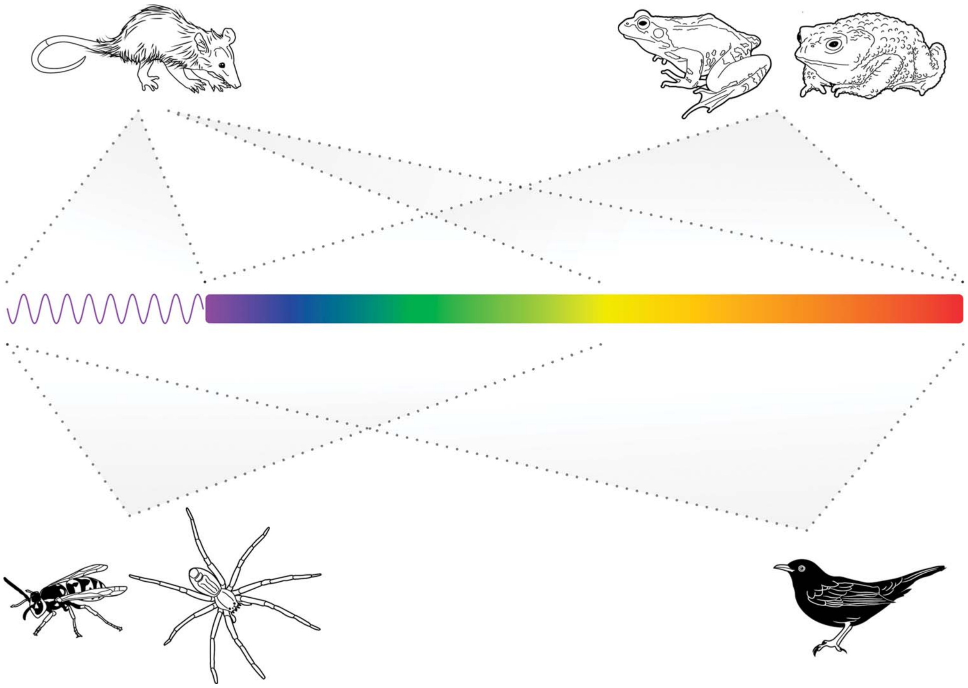


Figure 9.—Representation of spectral ranges that can be perceived by potential predators of harvesters. These ranges were based on the color vision of six species with records of predation or behavioral experiments: opossum (*Didelphis aurita*; UV and red receptors), frogs (*Rana temporaria* and *Bufo bufo*; blue, green, and red receptors), bird (*Turdus merula*; UV, blue, green and red receptors), spider (*Cupiennius salei*; UV, blue and green), and wasp (*Vespula germanica*; UV, blue and green receptors). The purple wavy live represents the UV range.

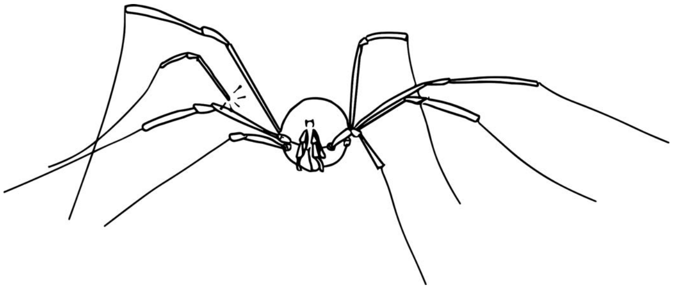


Figure 10.—Harvester from the suborder Eupnoi with leg III detached.

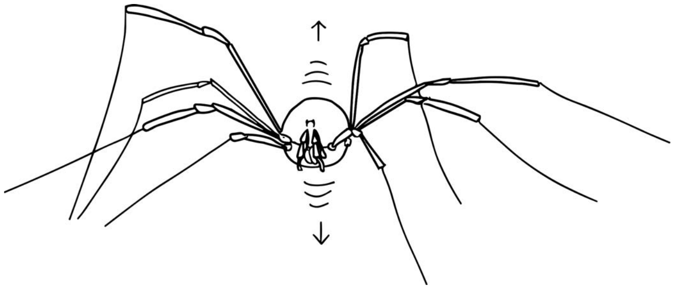


Figure 12.—Schematic representation of a harvester from the suborder Eupnoi, moving the body up and down, behavior known as bobbing.

point. Researchers have shown that chemical defenses were not used when harvesters were attacked by three species of spiders. However, the harvesters almost always survived the attacks: 33 out of 33 attacked by the scytodid *Scytodes globula* Nicolet, 1849, 38 out of 40 by the ctenid *Enoploctenus cyclothorax* (Bertkau, 1880), and 29 out of 34 by the ctenid *Ctenus ornatus* (Keyserling, 1877) (Souza & Willemart 2011; Carvalho et al. 2012; Dias & Willemart 2013). The spiders had in common that they did not bite specific areas of the body and most often ended up biting the armor. The authors have therefore raised the harvest-ironman hypothesis (Souza & Willemart 2011), which states that the thick cuticle forms an armor that protects these animals against some predators. They predicted that arthropod predators that somehow manage to avoid that armor would kill and consume harvesters. The recluse spider *Loxosceles* Heineken & Lowe, 1832 supported this prediction by attacking vulnerable parts of the armor such as the tips of the legs and articulations, and being successful (only 7 out of 38 harvesters survived attacks; Segovia et al. 2015a). A scorpion that attacked another vulnerable part (mouth) also successfully consumed most of the armored harvesters (23/58 harvesters survived; Albín & Toscano-Gadea 2015). Harvesters with similar defenses but with a soft exoskeleton should also be preyed upon by those spiders that do not avoid the armor, as was supported by large but immature harvesters, with thin cuticle (0 out of 9 survived; Dias & Willemart 2013). Anecdotal observations with 10 pairs of spiders that jump on the harvesters and do not select specific spots to bite have shown that these are also usually not successful (RHW, personal observation). Taken together, these data corroborate the harvest-ironman hypothesis.

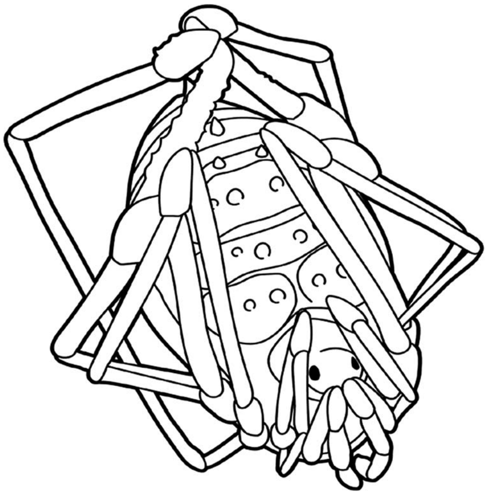


Figure 11.—Harvester in a motionless posture with legs retracted. Illustrated by Vítor Marques de Faria.

Chemical defense, surprisingly, was not even used against deadly recluse spiders (Segovia et al. 2015b) and was sometimes used but ignored by scorpions (Albín & Toscano-Gadea 2015). It was later shown, however, that chemicals are actually used (15/32 observations) and successfully repel predatory flatworms, against which the armor is useless (Silva et al. 2018). Other defensive mechanisms, such as pinching with spines on legs IV, have been observed against ctenids and recluse spiders (Fig. 13; Dias & Willemart 2013; Segovia et al. 2015b). Spines may perforate the integument of the predator and startle it but do not kill it. Pinching with legs IV (Fig. 13) was also successful in repelling flatworms and sometimes cutting them into two pieces (Silva et al. 2018).

In summary, the armor protects against some spiders, but not all, and certainly not against flatworms. As for chemicals, even if droplets experimentally applied to spiders may repel some of them, chemical defense is seldom used against spiders, even the deadliest ones (Segovia et al. 2015a). However, it is usually used successfully against flatworms. Pinching with legs IV is efficient against both, but also rarely used against spiders.

Several questions on when/which context/against which predators harvesters should use their defense are still open. For example, several species secrete chemicals when handled by the body but not by the legs, likely because chemicals are costly and volatiles may be inefficient. However, what about when the predator kills the harvester in 82% of the attacks by biting its legs, and the harvester species involved could have sprayed the defensive chemicals (Hara & Gnaspini 2003; Segovia et al. 2015a)? Why are the scent glands not used in this scenario? We can also consider spiders that do attack the body such as *Ctenus ornatus*: It killed harvesters in only 15% of the attacks, but dying is one of the ultimate costs. Why did harvesters not use their chemicals? It remains unclear how physiological features such as hunger, the amount of secretion a harvester has stored, predator density (i.e., the probability of encountering future predators), or the stimuli provided by the predator influence which defensive mechanism will be used. While these questions are still unanswered, the increasing number of researchers studying these animals is likely to shed light on this scenario in the future.

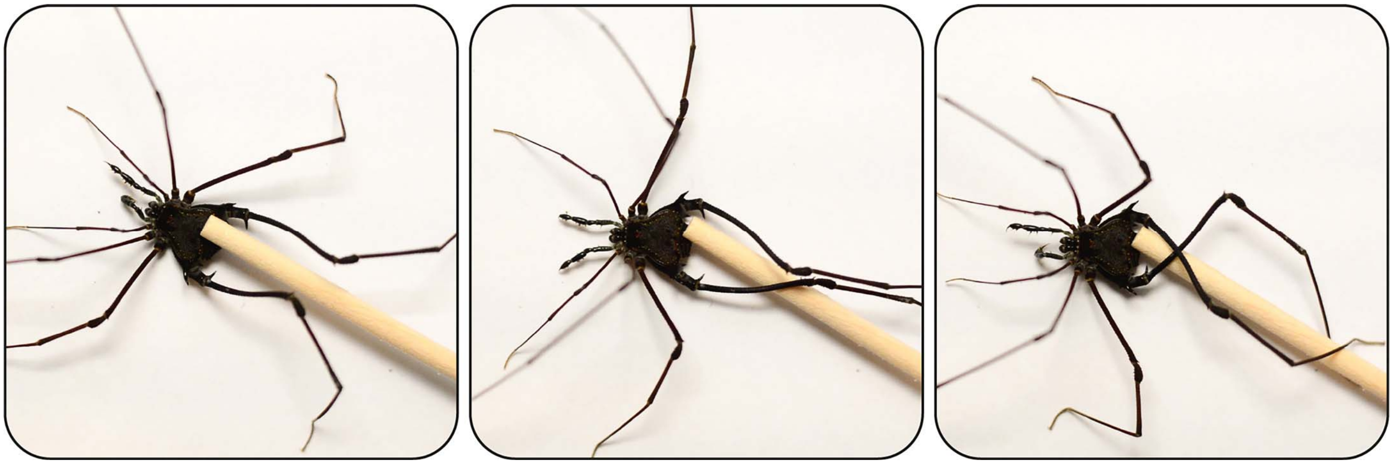


Figure 13.—Sequential photographs showing a laniatorid harvester pinching a stick with its legs IV. The sharp spines some species have on the internal region of the femur may perforate the aggressor.

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SUPPLEMENTAL MATERIALS

Supplemental File S1.—Opilionid chemicals, online at https://doi.org/10.1636/JoA-S-22-054.s1

LITERATURE CITED

Albín A, Toscano-Gadea CA. 2015. Predation among armored arachnids: *Bothriurus bonariensis* (Scorpions, Bothriuridae) versus four species of harvestmen (Harvestmen, Gonyleptidae). *Behavioural Processes* 121:1–7. https://doi.org/10.1016/j.beproc.2015.10.003

Baden T, Osorio D. 2019. The retinal basis of vertebrate color vision. *Annual Review of Vision Science* 5:177–200. https://doi.org/10.1146/annurev-vision-091718-014926

Barnett CA, Skelhorn J, Bateson M, Rowe C. 2012. Educated predators make strategic decisions to eat defended prey according to their toxin content. *Behavioral Ecology* 23:418–424. https://doi.org/10.1093/beheco/arr206

Caetano DS, Machado G. 2013. The ecological tale of Gonyleptidae (Arachnida, Opiliones) evolution: Phylogeny of a Neotropical lineage of armoured harvestmen using ecological, behavioural and chemical characters. *Cladistics* 29:589–609. https://doi.org/10.1111/cla.12009

Carvalho LA, Da Silva Souza E, Willemart RH. 2012. Behavioral analysis of the interaction between the spitting spider *Scytodes globula* (Araneae: Scytodidae) and the harvestman *Discocyrtus invalidus* (Opiliones: Gonyleptidae). *Journal of Arachnology* 40:332–337. https://doi.org/10.1636/Hill-86.1

Chelini MC, Willemart RH, Gnaspini P. 2011. Caves as a winter refuge by a neotropical harvestman (Arachnida, Opiliones). *Journal of Insect Behavior* 24:393–398. https://doi.org/10.1007/s10905-011-9264-x

Chelini MC, Willemart RH, Gnaspini P. 2012. Gregarious behavior of two species of Neotropical harvestmen (Arachnida: Opiliones: Gonyleptidae). *Journal of Arachnology* 40:256–258. https://doi.org/10.1636/Hi11-12.1

Chelini M, Willemart RH, Hebets EA. 2009. Costs and benefits of freezing behaviour in the harvestman *Eumesosoma roeweri*. *Behavioural Processes* 82:153–159. https://doi.org/10.1016/j.beproc.2009.06.001

Cokendolpher JC, Mitov PG. 2007. Natural enemies. Pp. 399–373. *In* Harvestmen: The Biology of Opiliones. (Pinto-da-Rocha R, Machado G, Giribet G (eds)). Harvard Univesity Press, Cambridge.

Cook DR, Smith AT, Proud DN, Víquez C, Townsend VR Jr. 2013. Defensive responses of Neotropical harvestmen (Arachnida, Opiliones) to generalist invertebrate predators. *Caribbean Journal of Science* 47: 325–334. https://doi.org/10.18475/cjos.v47i3.a20

Cuthill IC, Allen WL, Arbuckle K, Caspers B, Chaplin G, Hauber ME et al. 2017. The biology of color. *Science* 357, eaan0221. https://doi.org/10.1126/science.aan0221

Cuthill IC, Stevens M, Sheppard J, Maddocks T, Párraga CA, Troscianko TS. et al. 2005. Disruptive coloration and background pattern matching. *Nature* 434:72–74. https://doi.org/10.1038/nature03312

Dias BC, Willemart RH. 2013. The effectiveness of post-contact defenses in a prey with no pre-contact detection. *Zoology* 116:168–174. https://doi.org/10.1016/j.zool.2012.12.001

Domínguez M, Escalante I, Carrasco-Rueda F, Figuerola-Hernández CE, Ayup MM, Umaña MN, et al. 2016. Losing legs and walking hard: Effects of autotomy and different substrates in the locomotion of harvestmen in the genus *Prionostemma*. *Journal of Arachnology* 44:76–82. https://doi.org/10.1636/J15-08.1

Donaldson ZR, Grether GF. 2007. Tradition without social learning: Scent-mark-based communal roost formation in a Neotropical harvestman (*Prionostemma* sp.). *Behavioral Ecology and Sociobiology* 61: 801–809. https://doi.org/10.1007/s00265-006-0311-0

Emberts Z, Escalante I, Bateman PW. 2019. The ecology and evolution of autotomy. *Biological Reviews* 94:1881–1896. https://doi.org/10.1111/brv.12539

Escalante I, Albín A, Aisenberg A. 2013. Lacking sensory (rather than locomotive) legs affects locomotion but not food detection in the harvestman *Holmbergiana weyenberghi*. *Canadian Journal of Zoology* 91:726–731. https://doi.org/10.1139/cjz-2013-0098

Escalante I, Badger MA, Elias DO. 2020a. Rapid recovery of locomotor performance after leg loss in harvestmen. *Scientific Reports* 10:1–13. https://doi.org/10.1038/s41598-020-70557-2

Escalante I, Domínguez M, Gómez-Ruiz DA, Machado G. 2022. Benefits and costs of mixed-species aggregations in harvestmen (Arachnida:

Opiliones). *Frontiers in Ecology and Evolution* 9:1–24. https://doi.org/10.3389/fevo.2021.766323

Escalante I, Ellis VR, Elias DO. 2020b. Leg loss decreases endurance and increases oxygen consumption during locomotion in harvestmen. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology* 207:257–268. https://doi.org/10.1007/s00359-020-01455-1

Gnaspini P, Cavalheiro AJ. 1998. Chemical and behavioral defenses of a neotropical cavernicolous harvestman: *Goniosoma spelaeum* (Opiliones, Laniatores, Gonyleptidae). *Journal of Arachnology* 26:81–90.

Gnaspini P, Hara MR. 2007. Defense mechanisms. Pp. 374–399. *In* Harvestmen: The Biology of Opiliones. (Pinto-da-Rocha R, Machado G, Giribet G (eds)). Harvard University Press, Cambridge.

González A, Rossini C, Eisner T. 2004. Mimicry: imitative depiction of discharged defensive secretion on carapace of an opilionid. *Chemoecology* 14:5–7. https://doi.org/10.1007/s00049-003-0252-2

Grether GF, Aller TL, Grucky NK, Levi A, Antaky CC, Townsend VR Jr. 2014a. Species differences and geographic variation in the communal roosting behavior of *Prionostemma harvestmen* in Central American rainforests. *Journal of Arachnology* 42:257–267. https://doi.org/10.1636/j14-27.1

Grether GF, Levi A, Antaky C, Shier DM. 2014b. Communal roosting sites are potential ecological traps: Experimental evidence in a neotropical harvestman. *Behavioral Ecology and Sociobiology* 68:1629–1638. https://doi.org/10.1007/s00265-014-1771-2

Guffey C. 1999. Costs associated with leg autotomy in the harvestmen *Leiobunum nigripes* and *Leiobunum vittatum* (Arachnida: Opiliones). *Canadian Journal of Zoology* 77:824–830. https://doi.org/10.1139/z99-026

Hara MR, Gnaspini P. 2003. Comparative study of the defensive behavior and morphology of the gland opening area among harvestmen (Arachnida, Opiliones, Gonyleptidae) under a phylogenetic perspective. *Arthropod Structure and Development* 32:257–275. https://doi.org/10.1016/S1467-8039(03)00040-9

Houghton JE, Townsend VR, Proud DN. 2011. The ecological significance of leg autotomy for climbing temperate species of harvestmen (Arachnida, Opiliones, Sclerosomatidae). *Southeastern Naturalist* 10: 579–590. https://doi.org/10.1656/058.010.0401

Hunt DM, Chan J, Carvalho LS, Hokoc JN, Ferguson MC, Arrese CA et al. 2009. Cone visual pigments in two species of South American marsupials. *Gene* 433:50–55. https://doi.org/10.1016/j.gene.2008.12.006

Jacobs GH. 2012. The evolution of vertebrate color vision. Pp. 156–172. *In* Sensing in Nature. (López-Larrea C. (ed)). Springer, New York, [22399401]

Jones RW, López-González C, Varas C, Gaona-Escamilla L. 2016. Black bears feed on harvestmen (Opiliones) in northwestern Mexico. *Journal of Arachnology* 44:83–84. https://doi.org/10.1636/J15-37.1

Kelber A, Vorobyev M, Osorio D. 2003. Animal colour vision - behavioural tests and physiological concepts. *Biological reviews of the Cambridge Philosophical Society* 78:81–118. https://doi.org/10.1017/S1464793102005985

Machado G. 2002. Maternal care, defensive behavior, and sociality in neotropical *Goniosoma* harvestmen (Arachnida, Opiliones). *Insectes Sociaux* 49:388–393. https://doi.org/10.1007/PL00012663

Machado G, Pomini AM. 2008. Chemical and behavioral defenses of the neotropical harvestman *Camarana flavipalpi* (Arachnida: Opiliones). *Systematics and Ecology* 36:369–376. https://doi.org/10.1016/j.bse.2007.12.006

Machado G, Vasconcelos CHF. 1998. Multi-species aggregations in Neotropical harvestmen (Opiliones, Gonyleptidae). *Journal of Arachnology* 26:389–391.

Machado G, Vital DM. 2001. On the occurrence of epizoic algae and liverworts on the harvestmen *Neosadocus* aff. *variabilis* (Opiliones: Gonyleptidae). *Biotropica* 33:535–538.

Machado G, Bonato V, Oliveira PS. 2002. Alarm communication: A new function for the scent–gland secretion in harvestmen (Arachnida: Opiliones). *Naturwissenschaften* 89:357–360. https://doi.org/10.1007/s00114-002-0337-8

Machado G, Carrera PC, Pomini AM, Marsaioli AJ. 2005. Chemical defense in harvestmen (Arachnida, Opiliones): Do benzoquinone secretions deter invertebrate and vertebrate predators? *Journal of Chemical Ecology* 31:2519–2539. https://doi.org/10.1007/s10886-005-7611-0

Machado G, Macías-Ordóñez R. 2007. Social behavior. Pp. 400–413. *In* Harvestmen: The Biology of Opiliones. (Pinto-da-Rocha R, Machado G, Giribet G (eds)). Harvard University Press, Cambridge.

Mappes J, Marples N, Endler JA. 2005. The complex business of survival by aposematism. *Trends in Ecology and Evolution* 20:598–603. https://doi.org/10.1016/j.tree.2005.07.011

Marples NM, Speed MP, Thomas RJ. 2018. An individual-based profitability spectrum for understanding interactions between predators and their prey. *Biological Journal of the Linnean Society* 125:1–13. https://doi.org/10.1093/BIOLINNEAN/BLY088

Merilaita S, Scott-Samuel NE, Cuthill IC. 2017. How camouflage works. *Philosophical Transactions of the Royal Society B: Biological Sciences* 372:20160341. https://doi.org/10.1098/rstb.2016.0341

Nazareth TM, Machado G. 2015. Egg production constrains chemical defenses in a neotropical arachnid. *PLoS ONE* 10:1–14. https://doi.org/10.1371/journal.pone.0134908

Nazareth TM, Sudatti DB, Machado G. 2016. Chemical defense as a condition-dependent trait in harvestmen. *Journal of Chemical Ecology* 42:1047–1051. https://doi.org/10.1007/s10886-016-0749-0

Pagoti GF, Portela E, Campanha JS, Dias JM, Willemart RH. 2019. On the function of the spoon-shaped pedipalps of harvestmen in the family Cosmetidae (Opiliones, Laniatores). *Journal of Natural History* 53: 2087–2098. https://doi.org/10.1080/00222933.2019.1692086

Pankewitz F, Hilker M. 2008. Polyketides in insects: Ecological role of these widespread chemicals and evolutionary aspects of their biogenesis. *Biological Reviews* 83:209–226. https://doi.org/10.1111/j.1469-185X.2008.00040.x

Pasteels JM, Gregoire JC, Rowell-Rahier M. 1983. The chemical ecology of defense in arthropods. *Annual Review of Entomology* 28:263–289. https://doi.org/10.1146/annurev.en.28.010183.001403

Pekár S, Raspotnig G. 2022. Defences of arachnids: diversified arsenal used against range of enemies. *Entomologia Generalis* 42:663–679.

Pomini AM, Machado G, Pinto-da-Rocha R, Macías-Ordóñez R, Marsaioli AJ. 2010. Lines of defense in the harvestman *Hoplobunus mexicanus* (Arachnida: Opiliones): Aposematism, stridulation, thanatosis, and irritant chemicals. *Biochemical Systematics and Ecology* 38:300–308. https://doi.org/10.1016/j.bse.2010.03.003

Porto W, Pérez-González A. 2020. Beauty under the mud: Soil crypsis in new species of the Malagasy genus *Ankaratrix* (Opiliones: Triaenonychidae: Triaenobuninae). *Zoologischer Anzeiger* 287:198–216. https://doi.org/10.1016/j.jcz.2020.06.001

Powell EC, Painting CJ, Hickey AJ, Machado G, Holwell GI. 2021. Diet, predators, and defensive behaviors of New Zealand harvestmen (Opiliones: Neopilionidae). *Journal of Arachnology* 49:122–140.

Proud DN, Wade RR, Rock P, Townsend JrVR, Chavez DJ. 2012. Epizoic cyanobacteria associated with a Neotropical harvestman (Opiliones: Sclerosomatidae) from Costa Rica. *Journal of Arachnology* 40: 259–261.

Raspotnig G. 2012. Scent gland chemistry and chemosystematics in harvestmen. *Biologia Serbica* 34:5–18.

Raspotnig G, Anderl F, Kunert O, Schaider M, Brückner A, Schubert M, et al. 2020. A novel class of defensive compounds in harvestmen: hydroxy-γ - lactones from the phalangiid *Egaenus convexus*. *Journal of Natural Products* 83:3278–3286. https://doi.org/10.1021/acs.jnatprod.0c00277

Raspotnig G, Bodner M, Schäffer S, Koblmüller S, Schönhofer A, Karaman. 2015. Chemosystematics in the Opiliones (Arachnida): A comment on the evolutionary history of alkylphenols and benzoquinones in the scent gland secretions of Laniatores. *Cladistics* 31:202–209. https://doi.org/10.1111/cla.12079

Raspotnig G, Schaider M, Föttinger P, Komposch C, Karaman I. 2011. Nitrogen-containing compounds in the scent gland secretions of European cladonychiid harvestmen (Opiliones, Laniatores, Travunioidea). *Journal of Chemical Ecology* 37:912–921. https://doi.org/10.1007/s10886-011-9996-2

Raspotnig G, Schaider M, Föttinger P, Schönhofer A. 2017. A model for phylogenetic chemosystematics: Evolutionary history of quinones in the scent gland secretions of harvestmen. *Frontiers in Ecology and Evolution* 5:1–14. https://doi.org/10.3389/fevo.2017.00139

Raspotnig G, Schaider MG, Stabentheiner E, Lels HJ. 2014. On the enigmatic scent glands of dyspnoan harvestmen (Arachnida, Opiliones): first evidence for the production of volatile secretions. *Chemoecology* 24:43–55. https://doi.org/10.1007/s00049-014-0146-5

Rocha DFO, Wouters FC, Machado G, Marsaioli AJ. 2013a. First biosynthetic pathway of 1-hepten-3-one in *Iporangaia pustulosa* (Opiliones). *Scientific Reports* 3:4–9. https://doi.org/10.1038/srep03156

Rocha DFO, Wouters FC, Zampieri DS, Brocksom TJ, Machado G, Marsaioli AJ. 2013b. Harvestman phenols and benzoquinones: Characterisation and biosynthetic pathway. *Molecules* 18:11429–11451. https://doi.org/10.3390/molecules180911429

Roth LM, Eisner T. 1962. Chemical defenses of arthropods. *Annual Review of Entomology* 7:107–136. https://doi.org/10.1146/annurev.en.07.010162.000543

Ruxton GD, Sherratt TN, Speed MP. 2004. Avoiding Attack, First. Oxford University Press.

Saporito RA, Donnelly MA, Spande TF, Garraffo HM. 2012. A review of chemical ecology in poison frogs. *Chemoecology* 22:159–168. https://doi.org/10.1007/s00049-011-0088-0

Schaefer HM, Stobbe N. 2006. Disruptive coloration provides camouflage independent of background matching. *Proceedings of the Royal Society B: Biological Sciences* 273:2427–2432. https://doi.org/10.1098/rspb.2006.3615

Schaider M, Raspotnig G. 2009. Unusual organization of scent glands in *Trogulus tricarinatus* (Opiliones, Trogulidae): evidence for a non-defensive role. *Journal of Arachnology* 37:78–83. https://doi.org/10.1636/sh08-01.1

Schaider M, Komposch C, Stabentheiner E, Raspotnig G. 2011. Functional anatomy of scent glands in *Paranemastoma quadripunctatum* (Opiliones, Dyspnoi, Nemastomatidae). *Journal of Morphology* 272: 1182–1191. https://doi.org/10.1002/jmor.10973

Schaider M, Novak T, Komposch C, Leis HJ, Raspotnig G. 2018. Methyl-ketones in the scent glands of Opiliones: a chemical trait of cyphophthalmi retrieved in the dyspnoan *Nemastoma triste*. *Chemoecology* 28:61–67. https://doi.org/10.1007/s00049-018-0257-5

Segovia JMG, Del-claro K, Willemart RH. 2015a. Delicate fangs, smart killing: the predation strategy of the recluse spider. *Animal Behaviour* 101:169–177. https://doi.org/10.1016/j.anbehav.2014.12.025

Segovia JMG, Moura RR, Willemart RH. 2019a. Starvation decreases behavioral consistency in a Neotropical harvestman. *Acta Ethologica* 22:203–208. https://doi.org/10.1007/s10211-019-00327-5

Segovia JMG, Murayama GP, Ximenes NG. 2019b. Harvestmen are fearful in the light but not the darkness. *Journal of Arachnology* 47:396–398. https://doi.org/10.1636/0161-8202-47.3.396

Segovia JMG, Willemart RH, Del-Claro K. 2015b. Defences of a Neotropical harvestman against different levels of threat by the recluse spider. *Behaviour* 152:757–773. https://doi.org/10.1163/1568539X-00003252

Silva MS, Willemart RH, Carbayo F. 2018. Sticky flatworms (Platyhelminthes) kill armored harvestmen (Arachnida, Opiliones) but are not immune to the prey′s weapons. *Journal of Zoology* 306:88–94. https://doi.org/10.1111/jzo.12570

Skelhorn J, Halpin CG, Rowe C. 2016. Learning about aposematic prey. *Behavioral Ecology* 27:955–964. https://doi.org/10.1093/beheco/arw009

Souza E da S, Willemart RH. 2011. Harvest-ironman: Heavy armature, and not its defensive secretions, protects a harvestman against a spider. *Animal Behaviour* 81:127–133. https://doi.org/10.1016/j.anbehav.2010.09.023

Stevens M. 2013. Sensory Ecology, Behaviour, and Evolution, 1st ed. Oxford University Press, Oxford, UK

Stevens M, Merilaita S. 2009a. Animal camouflage: Current issues and new perspectives. *Philosophical Transactions of the Royal Society B: Biological Sciences* 364:423–427.

Stevens M, Merilaita S. 2009b. Defining disruptive coloration and distinguishing its functions. *Philosophical Transactions of the Royal Society B: Biological Sciences* 364:481–488.

Stevens M, Ruxton GD. 2012. Linking the evolution and form of warning coloration in nature. *Proceedings of the Royal Society B: Biological Sciences* 279:417–426. https://doi.org/10.1098/rspb.2011.1932

Townsend VR, Classen-Rodriguez L, Maloney TJ, Moore MK. 2019. Stridulation by cosmetid harvestmen (Arachnida: Opiliones). *Journal of Arachnology* 47:132–141

Townsend VR, Schaus MH, Zvonareva T, Illinik JJ, Evans JT. 2017. Leg injuries and wound repair among cosmetid harvestmen (Arachnida, Opiliones, Laniatores). *Journal of Morphology* 278:73–88. https://doi.org/10.1002/jmor.20620

van der Kooi CJ, Stavenga DG, Arikawa K, Belušič G, Kelber A. 2021. Evolution of insect color vision: from spectral sensitivity to visual ecology. *Annual Review of Entomology* 66:1–28.

Walla P, Barth FG, Eguchi E. 1996. Spectral sensitivity of single photoreceptor cells in the eyes of the ctenid spider *Cupiennius salei* Keys. *Zoological Science* 13:199–202. https://doi.org/10.2108/zsj.13.199

Willemart RH, Gnaspini P. 2004. Spatial distribution, mobility, gregariousness, and defensive behaviour in a Brazilian cave harvestman *Goniosoma albiscriptum* (Arachnida, Opiliones, Gonyleptidae). *Animal Biology* 54:221–235. https://doi.org/10.1163/1570756042484674

Wink M. 2019. Quinolizidine and pyrrolizidine alkaloid chemical ecology – a mini-review on their similarities and differences. *Journal of Chemical Ecology* 45:109–115. https://doi.org/10.1007/s10886-018-1005-6

Yovanovich CAM, Koskela SM, Nevala N, Kondrashev SL, Kelber A, Donner K. 2017. The dual rod system of amphibians supports colour discrimination at the absolute visual threshold. *Philosophical Transactions of the Royal Society B: Biological Sciences* 372:20160066. https://doi.org/10.1098/rstb.2016.0066

Zvereva EL, Kozlov MV. 2016. The costs and effectiveness of chemical defenses in herbivorous insects: A meta-analysis. *Ecological Monographs* 86:107–124. https://doi.org/10.1890/15-0911.1

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