

Bugs with backpacks deter vision-guided predation by jumping spiders

R. R. Jackson^{1,3} & S. D. Pollard^{2,3}

1 School of Biological Sciences, University of Canterbury, Christchurch, New Zealand

2 Canterbury Museum, Christchurch, New Zealand

3 International Centre of Insect Physiology and Ecology (ICIPE), Thomas Odhiambo Campus, P.O. Box 30, Mbita Point, Kenya

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Correspondence

Robert R. Jackson, School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch, New Zealand.
Email: r.jackson@zool.canterbury.ac.nz

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Abstract

As a case study of how insects use masks as a defence against vision-guided predators, an experimental study was carried out using *Acanthaspis petax*, a reduviid bug ('ant bug') that covers itself with a 'mask', or 'backpack', made from carcasses of its preferred prey (ants), and three salticid spider species, *Hyllus* sp., *Plexippus* sp. and *Thyene* sp., salticids being predators with exceptionally acute vision. The ant bugs and the salticids were from the Lake Victoria region of East Africa. In each test, a salticid was presented with a live bug or a lure made from a dead bug, with the mask removed ('naked') or intact ('masked'). Salticids made predatory responses to naked bugs significantly more often than to masked bugs. These findings suggest that salticids readily identify naked bugs as prey, but fail to identify masked bugs as prey.

Introduction

'Primary defence' is a term for adaptations used by prey to interfere with detection and identification by predators, whereas 'secondary defence' refers to how prey defend themselves when primary defence fails and the predator initiates a predatory attack (Edmunds, 1974). Primary defence is pre-emptive, often being in place even when the predator is not in the vicinity and generally corresponding to the idea of prey hiding from its predators. A wide range of animals apply material from the environment to their bodies ('masking'). Although it has often been suggested that the masks of these animals function as primary defence, experimental studies that test this hypothesis are scarce.

Perhaps the best-known examples of masking come from aquatic invertebrates. In freshwater habitats, the larvae of caddisflies (Trichoptera) encase themselves in tubes made from debris selected from the environment (Wiggins, 1997), but the best-known examples are marine. Decorator crabs (Decapoda: Majidae), for example, select various types of algae, sponges, bryozoans, corals and hydroids from their surrounding habitat and adhere these organisms to their dorsal surface (Getty & Hazlett, 1978; Wickstein, 1980, 1993; Chris, Woods & Page, 1999; Woods & Page, 1999). *Metapontonia fungicola* Bruce (Decapoda: Pontoninae) is a shrimp species that lives communally with corals and, when alarmed, it retreats between the sheets of coral septa and pulls the coral's soft tissues over its back like a curtain (Yamashiro, 1999). *Paracentrotus lividus* Lamarck is a sea urchin that covers itself with empty mussel shells (Richner &

Milinski, 2000). Carrier shells (Gastropoda: Xenophoridae) use specialized secretions to cement dead shells, shell fragments, coral pieces or stones to their shell (Underwood & Eichhorst, 2000; Prem *et al.*, 2001). Various crabs from the families Homolidae, Dromiidae, Laterillidae, Dorippidae and Tymolidae have modified fifth legs that they use for carrying shells, sponges, ascidians, hydroids or black corals over their backs (see Wickstein, 1993). Terrestrial insects also use masks. For example, *Gymnopholus* is a genus of weevils (Coleoptera: Curculionidae) that grow fungi, algae, lichens, liverworts and mosses on their elytra and on the tops of their heads (Gressitt, Samuelson & Vitt, 1968).

The example we chose to study is an assassin bug (Hemiptera: Reduviidae). Two types of masking by assassin bugs have been recognized (Ambrose, 1999): (1) 'natural camouflaging', where the bug puts sand pebbles, dust particles, foliage fragments, shed exoskeletons, egg shells, snail shells and other debris from the surroundings on its body; (2) corpse camouflaging, where the mask is made of the remains of the bug's prey. Some especially striking examples of corpse camouflaging are known from the nymphs of the reduviid genus *Acanthaspis*. These bugs prey on a variety of insects, but especially on ants, and they cover their bodies with the remains of their prey (Odhiambo, 1958; Livingstone & Ambrose, 1984). Typically, they capture prey by grabbing it with their legs, piercing it with their syringe-like mouthparts and using the 'syringe' to inject digestive enzymes and paralyzing saliva. The bug then proceeds to suck up the digested ant tissues from inside the ant's exoskeleton. Once finished, the assassin bug places what

remains of the ant, an empty shell, on its back. The ant carcass adheres because of fine adhesive threads that the bug secretes from its abdomen (Schuh & Slater, 1995; Ambrose, 1999).

It has often been suggested that assassin bug masks function in primary defence (Miller, 1956; Odhiambo, 1958; Mühlenberg & Maschwitz, 1976; Livingstone & Ambrose, 1984; Ambrose, 1986). However, with one notable exception, Brandt & Mahsberg (2002), there has been little in the way of experimental testing of this anti-predator hypothesis. These authors carried out experiments using West African ant bugs, *Acanthaspis* sp. and *Paredocola* sp., and three types of predators chosen on the basis of how they rely on different sensory systems for prey detection: African house geckos *Hemidactylus brooki* Hallowell, which rely strongly on vision, centipedes *Scolopendra morsitans* Linnaeus, which rely on tactile and chemical information from the prey, and selenopid spiders. They called the selenopids 'wall spiders' and chose them as representative of spiders that rely for prey detection primarily on air currents and substrate vibration. All three predators had apparent difficulty capturing masked ant bugs (i.e. ant bugs that were wearing a backpack made from ant carcasses) and less difficulty capturing naked ant bugs (i.e. ant bugs from which the backpack had been removed).

The wall spider readily attacked masked as well as naked ant bugs, presumably as a consequence of the air-current and surface-vibration cues from both types of ant bugs being similar. However, the spider captured and ate naked ant bugs more often than masked ant bugs. This is apparently because, when grabbed hold of by the spider, the mask came loose, leaving the spider with a mouthful of ant carcasses while the naked ant bug fled. The mask seemed to function against the spider as a secondary defence, in much the same way as the better-known example of lizards losing tails (Cooper & Vitt, 1991; Downes & Shine, 2001; Cooper, Perez-Mellado & Vitt, 2004).

The centipedes readily attacked naked ant bugs, after making contact with these bugs' bodies, but seemingly failed to identify the masked ant bug, probably because the mask kept the centipedes' tactile and chemoreceptors out of physical contact with the ant bug's cuticle (i.e. the ant bug's mask seems to function as a primary defence against this predator). The ant bug's mask seems to function as a primary defence against geckos as well, but via a different sensory modality. Geckos seemed to have difficulty in ascertaining by sight that the masked ant bug was prey.

It may not be surprising that Brandt & Mahsberg (2002) used a vertebrate as a representative vision-guided predator and used a spider as a representative predator that relies on substrate vibration and air currents. Most spiders have simple eyes and only rudimentary eyesight. However, salticids are a major exception. These spiders have unique, complex eyes (Land 1969*a,b*; Blest, O'Carroll & Carter, 1990) and spatial acuity exceeding that of many birds and approaching that of primates (Land 1972, 1974; Williams & McIntyre 1980; Harland & Jackson, 2000*a*, 2004). Uniquely among spiders, salticids can detect prey by sight, stalk until

close and then attack by making an accurately gauged leap (Forster, 1977, 1982; Jackson & Pollard, 1996).

Here, our objective is to extend Brandt & Mahsberg's (2002) study by using three salticid species as the vision-guided predators and carrying out a more extensive experimental study of how the ant bug's mask might function in primary defence. Our hypothesis is that *Acanthaspis petax* Stal, an ant-eating assassin bug from East Africa, conceals its identity from predatory salticids by using a mask constructed from the bodies of dead ants.

Materials and methods

General procedures

Our field site and laboratory were at Mbita Point, in western Kenya, at the Thomas Odhiambo Campus of the International Centre of Insect Physiology and Ecology (ICIPE). Mbita Point is 1200 m above sea level (0°25'–0°30'S by 34°10'–35°15'E), with 900 mm of rainfall per annum and a mean annual temperature of 27 °C. Bugs were collected from the field at Mbita Point as needed. Salticids were from cultures established from individuals of *Hyllus* sp., *Thyene* sp. and *Plexippus* sp. collected at Mbita Point (for standard salticid-laboratory procedures, see Jackson & Hallas, 1986). The laboratory photoperiod was L12 h:D12 h, with lights being switched on at 07:00 h, and the salticids' rearing environments were 'enriched' (spacious cages, meshwork of twigs within each cage; see Carducci & Jakob, 2000). All salticids were juveniles when tested (body length 9 mm) and had no previous experience with ants or *A. petax*.

Testing was carried out with live bugs and with motionless lures made from dead bugs. All bugs used in live tests were first fed on ants to satiation and then subjected to a 24 h fast. The rationale for the pre-trial treatment was to minimize differences in behaviour that might have resulted had the bugs' feeding histories been more variable.

Alternate-day testing (one of two ant-bug nymphs presented at a time, on successive days) was adopted. One of the two ant bugs had a backpack of ants (i.e. it was masked),



Figure 1 Two juvenile *Acanthaspis petax*: one without (left) and one with (right) a mask constructed of ant carcasses.

whereas the other did not have a backpack of ants (i.e. it was naked) (Fig. 1).

Each individual salticid, bug and lure and each individual ant bug were used for testing only once. Testing was always in the morning (08:00 h) (i.e. each salticid was used in two alternate-day trials and each ant bug was exposed to a salticid only once).

The two ant bugs to which an individual salticid was exposed were matched by size in one of two ways. In 'matched-body-length tests', the body length of each bug was 4 mm, but the mask made the masked bug plus its mask 2 mm longer (6 mm) than the naked bug. In 'naked-larger tests', the body length of the naked bug (6 mm) was longer than that of the masked bug's body length plus its mask (4 mm).

Bugs were assigned at random to the 'masked' or 'naked' group. Forceps were used to pull the mask off of the live bugs assigned to the naked group at 09:00 h on the day before testing. Sample sizes were standardized: 30 tests for each salticid species with each bug type and 35 for each salticid species with each lure type.

Apparatus and lures

The testing apparatus was a 'window cage' [wood frame with a sliding-glass piece fitting into grooves on the frame and a wood piece ('wall') covering the side of the frame opposite the window]. When living bugs were used, the cage was positioned horizontally (i.e. the window served as the cage top and the wall served as the cage floor) and there were no holes in the wall. The cage was positioned vertically when lures, instead of living bugs, were used (i.e. the window was the front of the cage and the wall was the back) (Fig. 2).

A hole (centred on the wall) is shown in Fig. 2, and this was used for testing with lures (i.e. masked lure on 1 day and naked lure on the next or the previous day, decided at random). The hole in the wall was 15 mm in diameter and was plugged with a cork that fitted flush with the inside surface of the wall. During testing, a motionless lure was positioned on a cork, facing downward.

There was a hole in the frame used for introducing the salticid into the cage and, in tests with living bugs, for introducing the bug into the cage. During tests with living bugs, the introduction hole was at one side of the cage (because the cage was positioned horizontal), but it was at the bottom of the cage during tests with lures because the cage was positioned vertical. With the cage vertical, the salticid entered the cage and walked up towards the lure, which meant that the salticid tended to enter the cage oriented towards the lure. However, in preliminary trials, having the cage vertical when living bugs were used was problematic because the bugs tended to stay in the corners of the cage. Placing the apparatus horizontal ensured that bugs actively walked around the apparatus during the tests, spending much of their time away from the corners and edges of the frame.

Methods for making lures were as in numerous earlier studies (see Wells, 1988; Jackson & Tarsitano, 1993). The

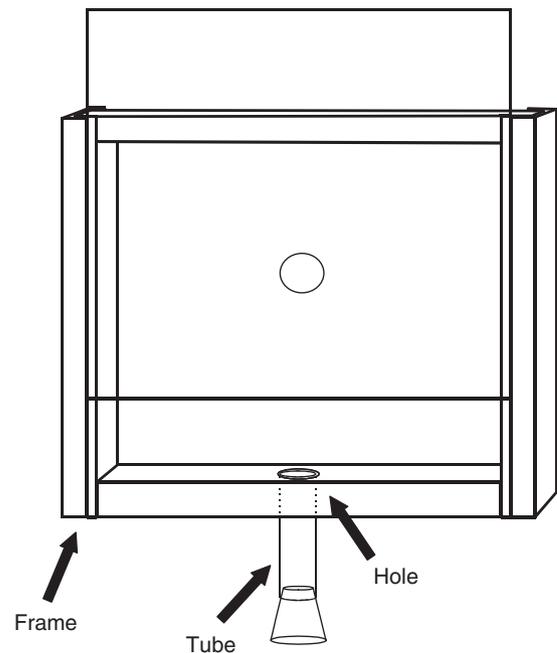


Figure 2 Cage for testing salticids with living ant bugs *Acanthaspis petax* and ant bug lures (230 mm × 225 mm × 60 mm wood frame). For tests with an ant bug lure, the lure was on a cork which was inserted through the hole shown in the centre of the wall.

bugs were killed with carbon dioxide gas, placed in ethanol (80%) for 60 min and then positioned in a life-like posture and glued onto a cork and sprayed with transparent varnish. The backpack was left on some of the bugs (masked), whereas the backpack was removed from others (naked). Whenever parts of the mask fell off the masked lure, testing with this lure was terminated.

Testing procedure

First the salticid or ant bug were taken into a small plastic tube. The tube was the same diameter as the hole in the frame of the cage. The salticid or bug was confined to the tube by a cork in each end. One of the corks was then taken from the tube and this end was inserted into the hole at the side of the cage. Once inserted, the other cork was removed and a paintbrush was inserted, gently coaxing the salticid or bug into the cage. The bug was introduced first followed by the salticid. The criterion for a successful test was that the salticid walked slowly out into the cage. If it ran or jumped about as it entered, then testing was aborted.

The predatory routine of the three African salticids resembled the routine typical for many salticids (Forster, 1979, 1982; Jackson & Pollard, 1996), with the primary stages usually being (1) fixate (the salticid orientates its cephalothorax so that the anterior medial eyes face directly towards the prey), (2) stalk (while fixated, the salticid walks directly towards the prey), (3) attack (by extending its rear legs, the salticid suddenly propels its body towards and forcefully contacts the prey).

We recorded whether or not the salticid made a predatory response during the test. The criterion for 'predatory response' when tested with live bugs was an attack. When testing with lures, the criterion was that the salticid stalked to within 10 mm of the lure, this criterion being adopted because, once within 10 mm of a lure, salticids often stopped stalking and walked away instead of attacking, suggesting that they discerned at a close range that the lure was not a living prey item. For data analysis, we used McNemar's tests for significance of change (for all comparisons, d.f. = 1) to compare tests with masked and naked bugs (see Zar, 1999).

Testing ended once a salticid made a predatory response (i.e. only one predatory response was permitted in a single test), and testing was aborted when, on rare occasions, a salticid that was not stalking came to within 5 mm from a living bug or a lure.

Results

Tests with living individuals of *A. petax*

When tested with masked ant bugs with a body length (including its mask) longer than the naked bug, significantly more salticids attacked naked ant bugs than masked ant bugs (McNemar's tests for significance of changes; $n = 30$ for each test): *Hyllus* sp., $\chi^2 = 7.68$, $P = 0.006$; *Thyene* sp., $\chi^2 = 6.41$, $P = 0.011$; *Plexippus* sp., $\chi^2 = 7.68$, $P = 0.006$ (Table 1). When the body length (plus the mask) of the masked bug was less than the body length of the naked bug, the salticids still attacked naked ant bugs significantly more often than masked ant bugs (McNemar; $n = 30$ for each test): *Hyllus* sp., $\chi^2 = 9.32$, $P = 0.002$; *Thyene* sp., $\chi^2 = 7.67$, $P < 0.01$; *Plexippus* sp., $\chi^2 = 13.42$, $P < 0.001$ (Table 2).

Tests with lures of *A. petax*

When tested with masked ant bugs with a body length (including its mask) longer than the naked bug, significantly more salticids attacked naked ant bugs than masked ant bugs (McNemar; $n = 35$ for each test): *Hyllus* sp., $\chi^2 = 14.34$, $P < 0.001$; *Thyene* sp., $\chi^2 = 10.27$, $P < 0.005$; *Plexippus* sp., $\chi^2 = 13.05$, $P < 0.001$ (Table 3). When the body length (plus the mask) of the masked bug was less than the body length of the naked bug, the salticids still stalked naked ant bugs significantly more often than masked ant

Table 1 Tests with living individuals of *Acanthaspis petax* (masked bug longer than naked bug)

Salticid species	Masked bug longer than naked bug	Salticid attacked bug	Salticid did not attack bug
<i>Hyllus</i>	Masked	1	29
	Naked	9	21
<i>Thyene</i>	Masked	1	29
	Naked	8	22
<i>Plexippus</i>	Masked	1	29
	Naked	9	21

Table 2 Tests with living individuals of *Acanthaspis petax* (masked bug shorter than naked bug)

Salticid species	Masked bug shorter than naked bug	Salticid attacked bug	Salticid did not attack bug
<i>Hyllus</i>	Masked	2	28
	Naked	12	18
<i>Thyene</i>	Masked	2	28
	Naked	10	20
<i>Plexippus</i>	Masked	1	29
	Naked	13	17

Table 3 Tests with lures of *Acanthaspis petax* (masked bug longer than naked bug)

Salticid species	Masked bug longer than naked bug	Salticid attacked bug	Salticid did not attack bug
<i>Hyllus</i>	Masked	1	34
	Naked	14	21
<i>Thyene</i>	Masked	2	33
	Naked	13	22
<i>Plexippus</i>	Masked	0	35
	Naked	11	24

Table 4 Tests with lures of *Acanthaspis petax* (masked bug shorter than naked bug)

Salticid species	Masked bug shorter than naked bug	Salticid attacked bug	Salticid did not attack bug
<i>Hyllus</i>	Masked	2	33
	Naked	15	20
<i>Thyene</i>	Masked	0	35
	Naked	12	23
<i>Plexippus</i>	Masked	3	32
	Naked	15	20

bugs (McNemar; $n = 35$ for each test): *Hyllus* sp., $\chi^2 = 13.13$, $P < 0.001$; *Thyene* sp., $\chi^2 = 14.48$, $P < 0.001$; *Plexippus* sp., $\chi^2 = 10.77$, $P < 0.005$ (Table 4).

Discussion

Brandt & Mahsberg (2002) used geckos to investigate whether the backpack functioned as a defence against vision-guided predators and they found that it did, but vertebrates are not the only animals that use acute vision to identify prey. In particular, salticids have eyes with spatial acuity closer to that of the best vertebrates and considerably better than that of other spiders and considerably better than that of the best insects (Land & Nilsson, 2002). Evidently, salticids have more difficulty identifying masked ant bugs as prey and less difficulty identifying naked ant bugs as prey. The experimental findings cannot be accounted for solely on the basis of prey size, as the findings

were consistent regardless of the relative size of the masked and naked bugs.

It might be argued that interpreting the findings from our live-bug testing, along with Brandt & Mahsberg's (2002) findings, was confounded by uncontrolled variables from the movement pattern, activity level and other behaviour of the bugs. Nothing that qualitatively suggested this was observed, but we, and Brandt & Mahsberg (2002), did not objectively record, or attempt to control, these variables when using living bugs. However, as in numerous earlier prey-choice studies using salticids (Jackson & Tarsitano, 1993; Li, Jackson & Cutler, 1996; Tarsitano & Jackson, 1997; Clark, Harland & Jackson, 2000; Harland & Jackson, 2000b), a strength of lure tests is that they control for these potentially confounding variables because, in these tests, there was no prey movement or other prey behaviour, and the only sensory cues available to the salticid were visual. Yet, the salticids stalked naked more often than masked lures.

It has been argued that predators tend to respond to basic aspects of the prey's characteristic form. The mask of the ant bug suggests that Robinson's hypothesis (Robinson, 1969) of bizarre forms may apply to bugs covered by ants. The idea of bizarre forms is that the prey hides the kinds of cues normally emanating from the characteristic form of typical prey and instead presents the predator with an appearance unlike any promising food object at all. This hypothesis has actually received little attention in the literature. Yet, this hypothesis appears relevant to the findings from this study where the vision-guided predators were salticids, along with Brandt & Mahsberg's (2002) findings where the vision-guided predators were geckos. On the whole, earlier studies of how masking might protect prey have envisaged the mask primarily as a facet of eucrypsis: once the animal has its 'mask' in place, it seems to blend in with a background similar to the mask (see Edmunds, 1974). However, the wall of the window cages used was not covered with ants, and it did not particularly resemble the appearance of the masked bugs. On the contrary, at least for human observers, masked bugs were readily detected on the wall. They just did not look like bugs. The hypothesis that these findings suggest is that the salticid readily detects the masked bug as an object separate from the background, but it fails to identify it as potential prey. A challenge for future research is to test this specific hypothesis.

As most salticids may be averse to preying on or coming close to ants (Nelson & Jackson, 2006), the fact that the bug's mask is normally made of ants may be important when the bugs encounter salticids. This hypothesis is currently being investigated (R. R. Jackson & S. D. Pollard, unpubl. data).

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