



## Predator–prey interaction between greenhead ants and processionary caterpillars is mediated by chemical defence



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The predatory greenhead ant, *Rhytidoponera metallica*, readily attacks some insects but not the processionary caterpillar, *Ochrogaster lunifer*. This urticarial lepidopteran larva is covered in long hairs and has numerous smaller, detachable barbed setae present on the third instar and older larvae. These setae are a health risk to humans and other mammals. In this study, we tested whether *O. lunifer* larvae are defended against invertebrate predators, using *R. metallica* as an example. Field experiments at *R. metallica* nests and laboratory olfactometer experiments were used to assess possible behavioural, morphological and chemical defence mechanisms. We found that a volatile chemical component from *O. lunifer* larvae inhibited attack/approach by *R. metallica*. This odour was associated with *O. lunifer* cuticular components: larval hairs, setae and exoskeleton. Behavioural defence was not found to inhibit *R. metallica* attack. Furthermore, despite the dense hairs and setae covering *O. lunifer* larvae, these did not act as a physical barrier to ant attack. Our study demonstrates the key role of chemical ecology in invertebrate interactions involving such hairy caterpillars. Future isolation of the deterrent chemical(s) produced by *O. lunifer* larvae may offer novel possibilities for managing ant behaviour.

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A variety of factors can cause mortality: environmental and pathological as well as predation. Chemically mediated defence is an example of protection from the latter and is common across phyla (Berenbaum, 1995). For example, herbivorous insects commonly sequester chemicals from host plants to make themselves unpalatable or repellent to potential predators (Bowers & Williams, 1995). Chemical defence is just one of the many defence mechanisms that Lepidoptera (butterflies and moths) have evolved in response to predation pressure (Montllor & Bernays, 1993). Other insect defence mechanisms include behaviours such as sound production (Bura, Fleming, & Yack, 2009), gregariousness, regurgitation and constructing shelters (Greeney, Dyer, & Smilanich, 2012). Some larvae have morphological traits such as thickened exoskeletons (Greeney et al., 2012) and cuticular spines or hairs for physical protection (Kageyama & Sugiura, 2016).

Larvae of the moth *Ochrogaster lunifer* (Lepidoptera: Notodontidae) exhibit some of the defence traits listed above, such as hairiness and living gregariously in constructed nests (Floater,

1996; Perkins et al., 2015). The larvae also have small (ca. 50–400 µm) detachable setae (modified hairs) on the third to eighth instar (Perkins et al., 2015) which cause medical problems in humans, including urticaria (itchiness and irritation of the skin) which occurs immediately after exposure, and dermatitis and allergic reaction thereafter (Battisti, Holm, Fagrell, & Larsson, 2011; Floater, 1996). *Ochrogaster lunifer* larvae are also responsible for miscarriages in horses when accidentally consumed by pregnant mares (Cawdell-Smith, Todhunter, Anderson, Perkins, & Bryden, 2012). Despite its medical and veterinary importance, and apparent significance to vertebrates, there is little information about *O. lunifer* ecology, including interactions with potential predators.

A prey species may be required to defend itself against multiple taxa, for example vertebrate and invertebrate predators. In such an instance the question can be asked, does the defence strategy developed demonstrate some level of parsimony? *Ochrogaster lunifer* larvae have urticarial setae that appear to mediate a pre-emptive chemical defence against mammals. They provide, therefore, an opportunity to determine how defence is mounted against invertebrates and whether the species uses a similar strategy for both vertebrate and invertebrate threat, presumably reducing the overall cost of resource allocation.

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Several invertebrate predators and parasitoids have been recorded for *O. lunifer*, including dermestid beetles, predatory pyrrhocorid bugs, chalcid wasps and tachinid flies (Floater, 1996). Ants have been observed attacking *O. lunifer* larvae while they ascended and descended host trees (Mills, 1951); however, in an earlier report, small ants were observed making a detour around *O. lunifer* larvae (Mills, 1950). More recently, an *O. lunifer* procession crossing a southern meat ant, *Iridomyrmex purpureus*, nest was not interfered with or attacked (M. P. Zalucki, personal observation). These contradictory observations of attack and avoidance behaviours by ants have not been tested experimentally.

Ants are recognized as important predators of insects in both agricultural and natural ecosystems (Osborn & Jaffe, 1998). Many ant species are abundant in *O. lunifer* habitats (M. Uemura, personal observation), including the omnivorous greenhead ant, *Rhytidoponera metallica* (Hymenoptera: Formicidae) which feeds on insects and other protein sources (Wenzel, 2011). No insect defence mechanism is effective against all potential predators (Sugiura & Yamazaki, 2014); however, there is a suite of mechanisms considered effective against generalist predators such as ants. One study on 70 species of lepidopteran larvae (not the focal species in this study) showed that hairs as a morphological trait deterred predation by a species of bullet ant, *Paraponera clavata* (Dyer, 1995). Numerous studies have demonstrated ants being repelled by nonspecific volatiles produced from glandular secretions and contact chemical irritants in insect prey (Osborn & Jaffe, 1998; Wenzel, 2011).

To understand more about *O. lunifer* defence against predation, our aims in this study were (1) to test whether ants from nests close to *O. lunifer* nests are predators of lepidopteran larvae in general, and of *O. lunifer* larvae in particular, and (2) if not, to determine through a series of simple experiments which defence mechanisms are used by *O. lunifer* larvae against ants: behavioural, morphological, chemical or volatile chemical. We conducted both manipulative field experiments and laboratory olfactometer studies.

## METHODS

### Field Study Sites

Ants are social insects and behave differently if removed from their nest (Koto, Mersch, Hollis, & Keller, 2015). Therefore, where possible, ant–bait interactions were studied in the field during October 2015–March 2016 at The University of Queensland (UQ), Gatton campus, Queensland, Australia (−27°56'S, 152°34'E). *Rhytidoponera metallica* ants are appropriate omnivorous predators for these experiments because they exhibit a feeding preference for insects (Wenzel, 2011), co-occur in *O. lunifer* habitats and are easily observed due to their relatively large size. Study sites were at active *R. metallica* nests in the vicinity (<25 m) of known *O. lunifer* larval nests. Eleven ant nests were identified (Nests A to K) and used throughout the experiments. Variability between ant nests, e.g. genetics, nutritional status, reproductive state and population number, was not controlled, but individual ant nests were included as a variable in the analysis. The effect of nest on the proportion of ants interacting with prey (as a gauge of nest activity) was evaluated and no individual nest differed significantly in its number of interactions (Appendix Table A1). Experiments were undertaken in dry conditions and temperatures above 28 °C between the hours of 0800 and 1630 local time.

### Insects

Second-instar ( $N = 100$ ) and fifth-instar ( $N = 75$ ) *O. lunifer* larvae were collected from nests on *Acacia* sp. trees at UQ Gatton campus, Queensland, and Draper, Queensland (−27°34'S, 152°90'E), respectively. Hairs and setae were obtained from

seventh-instar *O. lunifer* larvae collected from an *Acacia* sp. tree at UQ Gatton campus. Hairs fully cover the larval body, whereas setae are found in tight bunches on the abdominal segments (Perkins et al., 2015). *Rhytidoponera metallica* ants used in laboratory olfactometer studies were collected from nests in the field.

### Ethical Note

Only necessary numbers of *O. lunifer* larvae and *R. metallica* were collected to conduct the experiments. Ants and larvae were housed in breathable plastic containers with food and water changed regularly. In experiments involving immersion of larvae in hexane or water (see below), the larvae were euthanized prior to treatment. All other larvae and ants were euthanized immediately after each experiment. Euthanasia was performed by placing them into a −20 °C freezer overnight. Euthanized untreated larvae were kept for other experiments and analyses outside of this study.

### Predator–Prey Interaction Experiment

Live fifth- to sixth-instar *Helicoverpa armigera* (Lepidoptera: Noctuidae) larvae were used as bait to test the ant's interaction with a nonhairy palatable caterpillar. *Helicoverpa armigera* were cultured (following Perkins, Cribb, Hanan, & Zalucki, 2010) at UQ St Lucia campus, Queensland, Australia. The area surrounding an *R. metallica* nest entrance was divided into four to eight sectors, depending on the size of the nest and/or obstructions, which were assigned numbers (Appendix Fig. A1). Quadrats of 30 × 30 cm were used as experimental arenas and placed 50 cm away from the nest entrance within a numbered sector, selected randomly (see description of measurement variables below). The bait was placed in the middle of the quadrat, and ants in the quadrat were observed for 5 min or until the bait was carried outside the quadrat, if that happened sooner. Six or fewer ants were in the quadrat at any time and each was tracked visually to avoid counting the same ant twice. In other studies, ants are often marked for identification or removed, but we did not use these methods as the risk of pseudoreplication was low and we did not want to introduce a factor that could impact behavioural interactions. Ants in 20 quadrats were observed for *H. armigera*. Live second- and fifth-instar *O. lunifer* larvae were used as bait in 30 quadrats each. We recorded the total number of quadrats with ants interacting with the bait within a 5 min period.

### Field Experiments 1–3

Each experiment followed the same procedure as above but differed in the type of bait (Table 1). This was placed in the middle of the quadrat, and ants in the quadrat were observed for 5 min or until the bait was carried outside the quadrat, if that happened sooner. Hairs were present in all the second- and fifth-instar *O. lunifer* larvae we used, both dead and alive, unless stated otherwise (see below). Setae were only present in fifth-instar *O. lunifer* larvae.

The behavioural response of each ant towards the bait was classified as either rejection, attack or no interaction (see *Classification of ant behavioural responses*). For each bait, the behaviour of ants was classified within 30 quadrats (placed at five or more ant nests). The foraging behaviour of colony conspecifics was unlikely to impact individual behaviour, because *R. metallica* are solitary foragers and do not recruit other conspecifics by returning to the nest nor do they produce a pheromone trail (Thomas & Framenau, 2005). As ants are ectothermic, we recorded temperature and humidity data using a Tinytag Plus 2 data-logger TGP-4505 (Hastings Data Loggers, Port Macquarie, Australia) in situ for every trial. We used these data to determine whether environmental factors had

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