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NOTE

Differences in the behaviour of model and non-model species of ants in interactions with the pod-sucking myrmecomorphic bug, *Riptortus linearis* (Hemiptera: Alydidae)

Joy Nivedita SAMUEL and Neelkamal RASTOGI*

Department of Zoology, Institute of Science, Banaras Hindu University, Varanasi, 221 005, U.P., India;
e-mails: joy.samuel17@gmail.com, neelkamalrastogi@yahoo.co.in

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Abstract. Ants are common invertebrate models of many myrmecomorphic arthropods since they are unpalatable and pose a threat for many species. Natural habitats harbour a diverse community of different species of ants and their mimics. The myrmecomorphic bug, *Riptortus linearis* uses a variety of extrafloral nectary-bearing or hemipteran-harbouring legumes as host plants, which are also visited by various sugar-loving species of ants. In the present study, we investigated the responses of the ant-mimicking and non-mimicking stages of the pod-sucking bug, *Riptortus linearis,* its ant model, *Camponotus compressus* and a co-occurring ant, *Crematogaster subnuda*, during experimental encounters, under laboratory conditions. *Cr. subnuda* ants were much more aggressive than *Ca. compressus* ants towards the myrmecomorphic bug. However, the pod-sucking bug exhibited similar responses to both of the species of ants. More importantly, *Ca. compressus* ants did not bite the first instar nymph of the bug. The results of this study show that the non-model ant was significantly more aggressive than the ant model towards different stages of *R. linearis*. These results have important implications for the management of the pod-sucking bug, *R. linearis,* which is an important pest of many legumes.

INTRODUCTION

Ants are not only one of the most widespread insect taxa in terrestrial ecosystems, but also occupy diverse trophic levels and include both ground-dwelling and arboreal species, and as they are aggressive, noxious and unpalatable, are usually avoided by generalist predators (Pekár et al., 2017). Depending upon the species, ants can bite, sting, spray chemicals and rapidly recruit reinforcements (Hölldobler & Wilson, 1990). Many species of ants are models for many myrmecomorphic (ant mimicking) arthropods, including spiders, beetles, mantids, true bugs and crickets (Kumari & Rastogi, 2018; McLean et al., 2019). Myrmecomorphy is reported to occur in more than 2000 species of arthropods belonging to 200 genera and 54 families (McIver & Stonedahl, 1993).

Myrmecomorphs are arthropods that resemble ants since this has various advantages such as protection from predators or access to food (Cushing, 2012). The basis of this adaptive strategy is Batesian mimicry, as vulnerable and palatable arthropods deceive their predators by resembling aggressive and noxious ants (Ruxton et al., 2004). Several species of Hemiptera, belonging to the families Miridae (Jackson & Drummond, 1974) and Alydidae (Oliveira, 1985) are known to resemble ants (Kumari & Rastogi, 2018). Many of these species undergo transformational mimicry in which only the vulnerable and wingless nymphs mimic ants (McIver & Stonedahl, 2008). For instance, the alydid bug, *Riptortus serripes* (Fabricius, 1775) (Hemiptera: Alydidae), is an excellent example of transformational myrmecomorphy, as it is only the nymphs that resemble *Oecophylla smaragdina* (Fabricius, 1860) (Hymenoptera: Formicidae) and the adults do not resemble an ant at all (Ceccarelli, 2009). This may be because winged adults can escape predators much more easily than wingless nymphs (Ceccarelli, 2009). The pod-sucking bug, *Riptortus linearis*, which feeds on many economically important leguminous plants, is reported to be a transformational mimic of workers of *Camponotus compressus* (Fabricius) (Hymenoptera: Formicidae). These plants are also visited by several other species of ants, including *Crematogaster subnuda* (Kumari & Rastogi, 2018) (Fig. 1A–B). Eggs of *R. linearis* are laid singly on leaves and pods (pers. obs.) and hatch and undergo five instars before becoming winged adults (Fig. 1 C–F).

The myrmecomorphic bug adaptively uses workers of *Ca. compressus* as its model probably because *Ca. compressus* is often not only the most commonly recorded plant-visiting species of ant, but is also the most abundant (Kumari & Rastogi, 2018). Hence, mimicry of *Ca. compressus* worker ants is likely to enable the bug to avoid detection by potential visual predators. Many species of ants, especially those belonging to the genus *Camponotus* are unpalatable due to the defensive secretion of formic

* Corresponding author; e-mail: neelkamalrastogi@yahoo.co.in

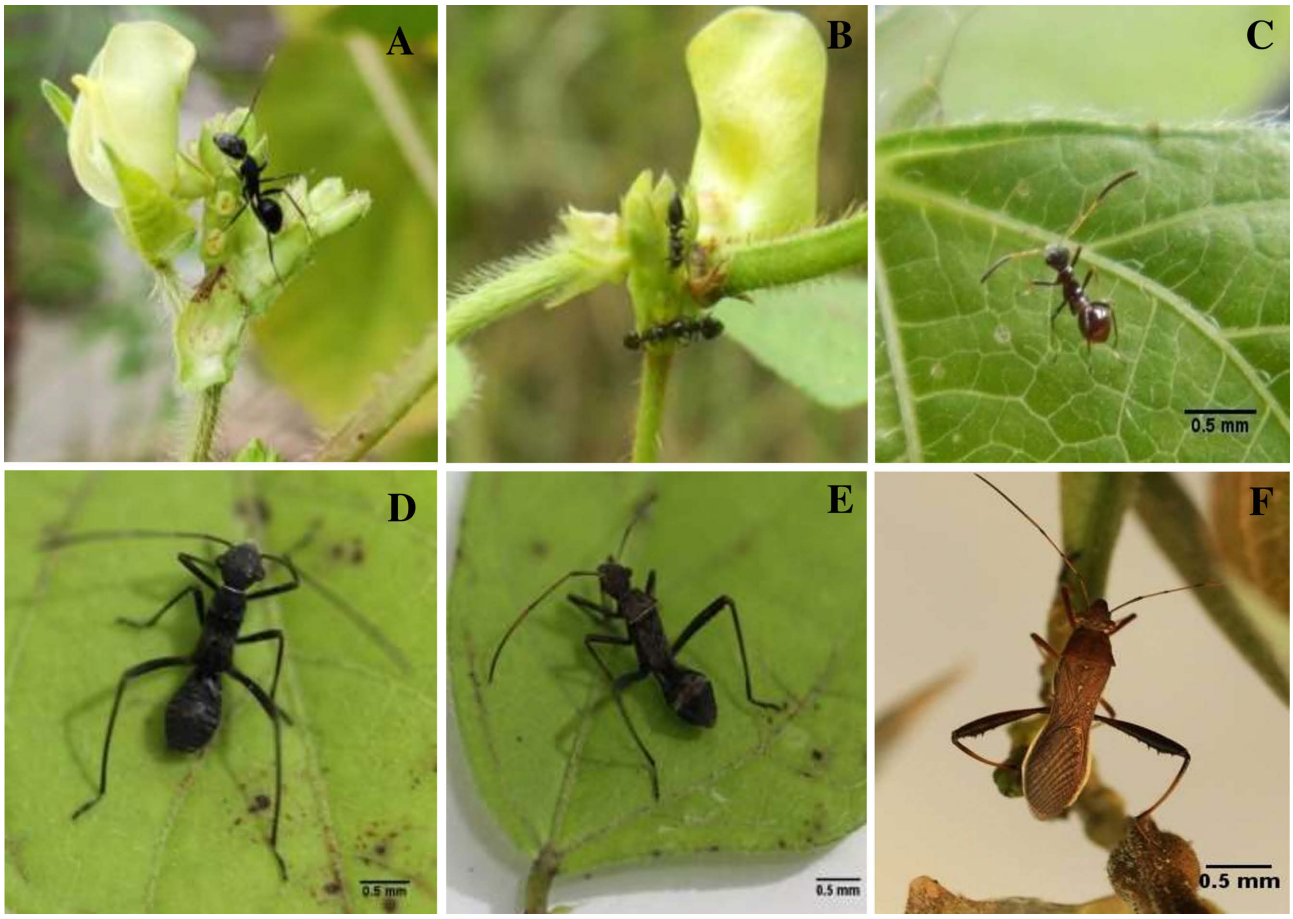

Fig. 1. The ant model. A – *Camponotus compressus*, non-model; B – *Cematogaster subnuda*, different ant-mimicking stages of *Riptortus linearis*: C – first, D – third and E – fifth nymphal instars, and F – the non-mimicking adult.

acid. Therefore, the majority of predators avoid eating ants. For Batesian mimicry to be a successful anti-predator strategy, the ant model should be less aggressive towards its mimic than to other plant-visiting (non-model) species of ants. This may evolve if the model and the mimic (which do not compete for similar resources) frequently encounter one another on plants. This needs to be confirmed by recording the behaviour of each of the interacting species (mimic, non-mimic, model and non-model species of ants) in inter-specific confrontation experiments.

Therefore, we hypothesise that while myrmecomorphic bugs should remain in close vicinity of their model, in order to avoid being attacked by other aggressive species of ants, the mimics should avoid close encounters with non-model species of ants. We recorded the behavioural responses of the ants and bugs in laboratory-based interactions between various stages of *R. linearis* and each of the two co-occurring species of ants, *Ca. compressus* (previously reported to be its model) and *Cr. subnuda* (which is not its model). We addressed the following questions: (1) Does the non-model, *Cr. subnuda* and model, *Ca. compressus* respond differently to the various stages of *R. linearis*? and (2) Does the ant-mimicking nymphs and non-mimicking adult stages of *R. linearis* respond differently to the model and non-model species of ant?

MATERIALS AND METHODS

Four different stages (first, third and fifth instar nymphs and adults) of the bug, *R. linearis* and workers of two species of ants, *Ca. compressus* and *Cr. subnuda*, were collected (August to October, 2019), from pod-bearing potted *Vigna radiata* (Fabaceae) plants, grown in the botanical garden of Banaras Hindu University campus in Varanasi, U.P. in India. All the insects were collected on the day of the experiment, transferred into individual containers (each with a finely perforated lid) and brought to the laboratory.

Confrontation experiments (duration of each observation = 15 min, n = 25, per stage per species of ant) were carried out in Petri dishes in which the behavioural responses of the worker ants of *Ca. compressus* (the ant model) and *Cr. subnuda* (the non-model ant species) to the ant-mimicking first, third and fifth instars and non- mimicking adults of *R. linearis* were recorded and *vice versa*. Petri dishes (10 cm × 2.5 cm) were used for recording the pair-wise interactions between each of the four specific stages of the bug and each of the two species of ants. A single worker ant (*Ca. compressus/Cr. subnuda*) was placed in a Petri dish and allowed to acclimatize for five minutes. In the next step, a single bug of a specific stage was placed in the same Petri dish in the side opposite to where the ant was present and the behaviour of each was observed and recorded. The behavioural response of each interacting insect was placed in one of three categories as follows: (1) Neutral – 'touching' (if the ant touches the bug with its antennae); 'ignore' (on encountering the bug, the ant stops and remains there briefly without showing any other activity), 'remain still' (remains in the same position even after the interaction); (2) Aggressive – 'bite' (ant bites the bug with its mandibles); (3) Submissive – 'avoid' (the bug suddenly changes the direction of movement on encountering the ant) and 'flight response' (following an encounter the bug rapidly runs or flies away from the ant).

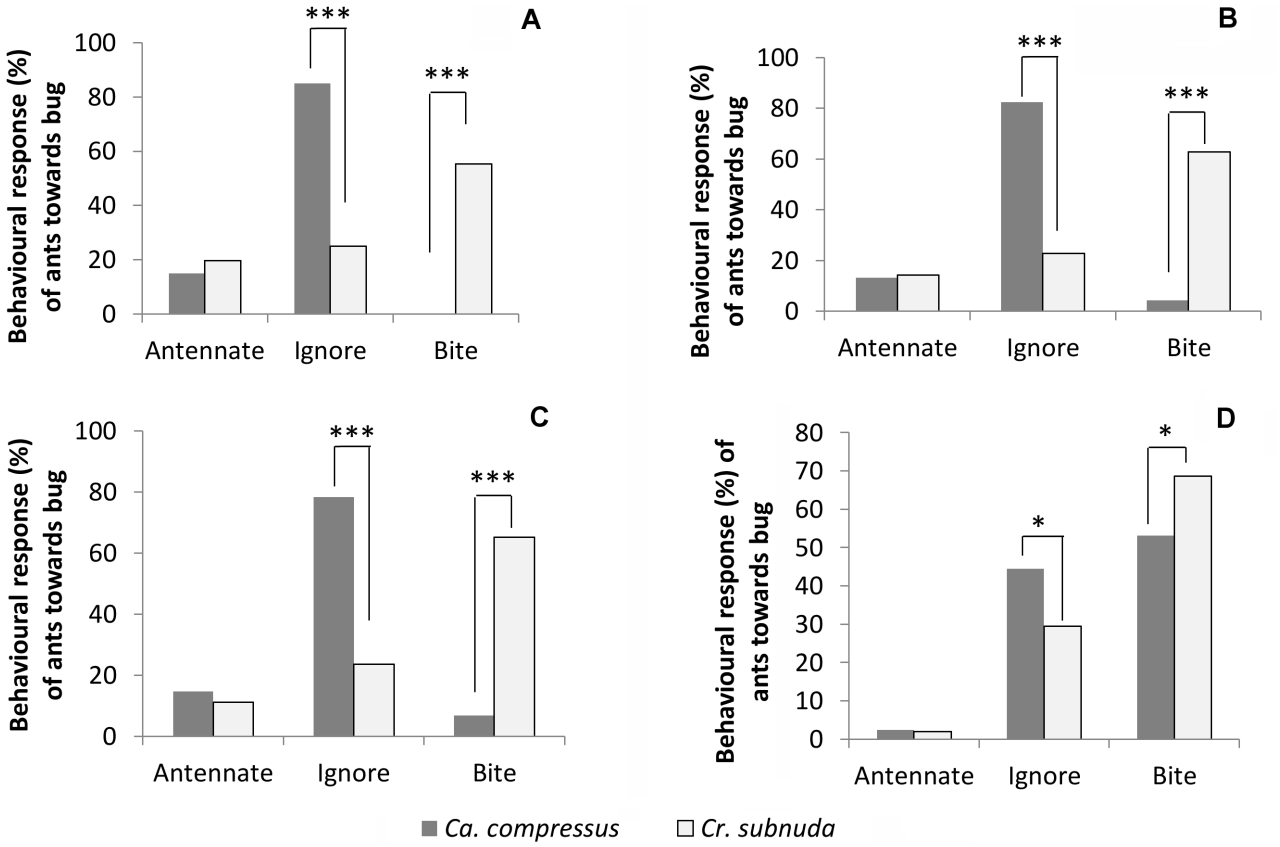

Fig. 2. Behavioural responses (%) of the ants *Camponotus compressus* and *Crematogaster subnuda* to: A – first, B – third and C – fifth ant-mimicking nymphal instars and D – the non-mimicking adult of *Riptortus linearis* in the laboratory. Chi square test: P < 0.05.

A chi-square test was used to analyse: (1) the behavioural responses (in %) of each of the two species of ant to each of four stages of *R. linearis*, and (2) the behavioural responses (in %) of each of the four stages of *R. linearis* to each of the two species of ant.

RESULTS

The responses of worker ants of *Ca. compressus* were either neutral (touching with antennae or ignoring) or aggressive (biting) on encountering the nymphs and adult stages of *R. linearis*; the only exception was the first instar nymph of the bug, which did not elicit either aggression or biting by this ant. *Cr. subnuda* were more often aggressive than neutral towards all stages, including the first instar nymphs of *R. linearis* (Fig. 2). In a high percentage of encounters with the adult stage of the bug, each of the two species of ants was observed to lunge with extended mandibles and bite it. The two species of ants differed significantly in the level of aggressive behaviour displayed towards the various stages of the bug. *Ca. compressus* ants 'ignored' all three instars of nymphs, first ($\chi^2 = 72.73$, $P < 0.001$, d.f. = 1), third ($\chi^2 = 69.79$, $P < 0.001$, d.f. = 1) and the fifth instars ($\chi^2 = 58.34$, $P < 0.001$, d.f. = 1) and adults ($\chi^2 = 4.85$, $P < 0.05$, d.f. = 1) of *R. linearis*, significantly more than *Cr. subnuda*. Analyses of the biting behaviour of the two ants revealed that *Cr. subnuda* worker ants bite the first ($\chi^2 = 75.86$, $P < 0.001$, d.f. = 1), third ($\chi^2 = 78.13$, $P < 0.001$, d.f. = 1), fifth instars ($\chi^2 = 73.00$, $P < 0.001$, d.f. = 1) and adult ($\chi^2 = 4.75$, $P < 0.05$, d.f. = 1) *R. linearis*, significantly more than *Ca. compressus*. *Ca. compressus* did not bite the first instar nymph even once, during the behavioural interactions. No significant differences were found in the "touching" behaviour of the two species of ants towards any stage of the bug (Fig. 2).

On being confronted by each of the two species of ants the nymphs and the adults of the bug either showed neutral behaviour by 'remaining still' or submissive behaviour by showing an 'avoid' or 'flight response'. All the three instar nymphs of *R. linearis* showed significantly more 'remain still' response towards *Cr. subnuda* than *Ca. compressus* (first instar: $\chi^2 = 4.48$ P < 0.01; third instar: 5.89, P < 0.01; fifth instar: 10.88, $P < 0.001$; d.f. = 1 in each case). Also, all the nymphs avoided *Ca. compressus* significantly more (first instar: $\chi^2 = 16.33$; third instar: 25.13; fifth instar: 25.13, $P < 0.001$ & d.f. = 1 in each case) than *Cr. subnuda*. The behavioural responses of the adult bug towards the two species of ants were not significantly different. There was no significant difference between the flight response of any stage of the bug on encountering each of the two species of ants although the percentage exhibiting a flight response was the highest in case of the first instar (*Ca. compressus*: 54%, *Cr. subnuda*: 74.2%) and lowest in the case of the adult (*Ca. compressus*: 33.34%, *Cr. subnuda*: 34.57%) of the bug (Fig. 3).

DISCUSSION

The results revealed marked difference between the behaviour of the two ants towards the nymphs and adults of the myrmecomorphic bug *R. linearis*. The response of *Ca. compressus*, the ant model of the myrmecomorphic nymphs of the pod-sucking bug, was significantly neutral. Most *Ca. compressus* ants ignored them while *Cr. subnuda* was significantly more aggressive towards the nymphs of the pod-sucking bug. While the adaptive basis of successful Batesian mimicry involves deceiving potential predators, it is expected to be still more effective if the mimic is able to move around and feed on its host plant close to its model, which does not harm it. Lower levels of aggression shown by the

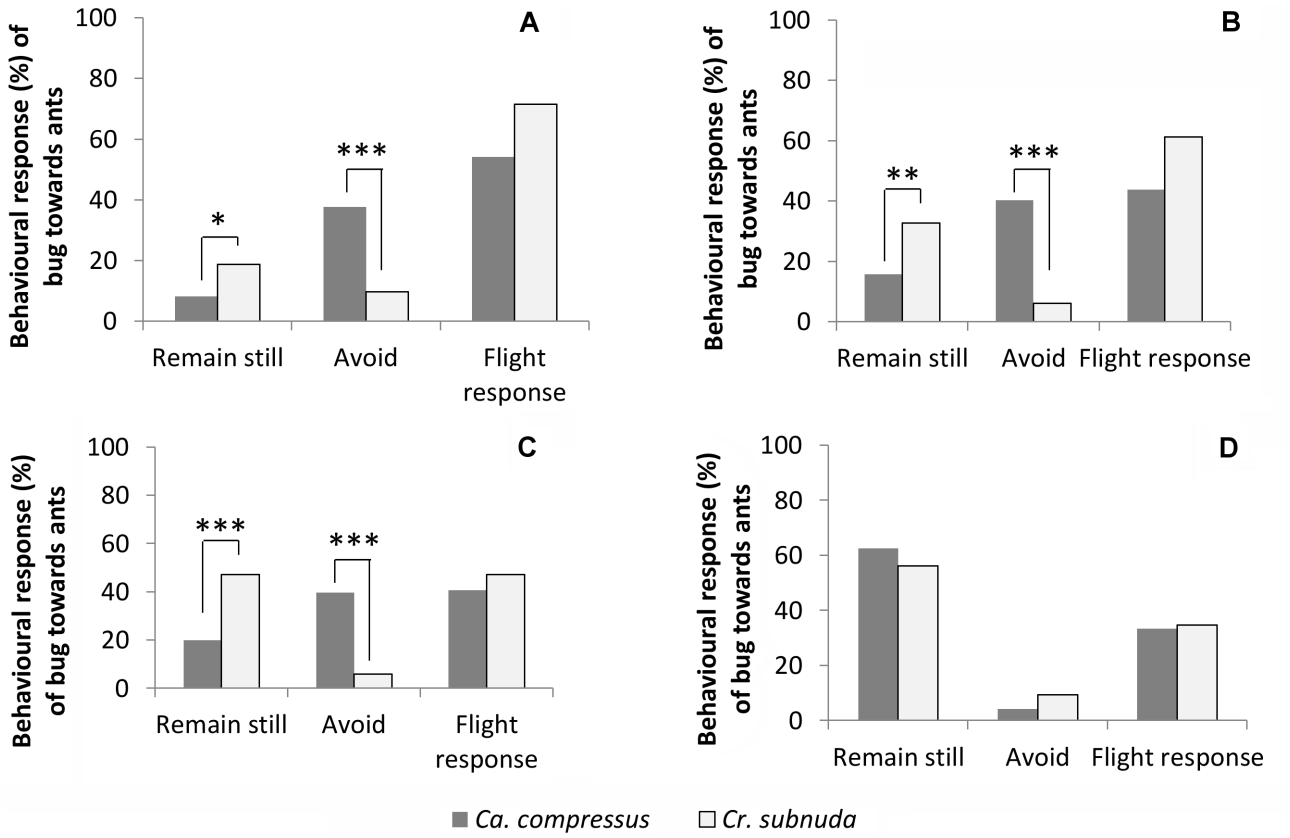

Fig. 3. Behavioural responses (%) of A – first, B – third and C – fifth ant-mimicking nymphal instars, and D – the non-mimicking adult of *Riptortus linearis* to *Camponotus compressus* and *Crematogaster subnuda* in the laboratory. Chi square test: $P < 0.05$.

ant model (as compared to the non-model ant) may also account for the fact that the myrmecomorphic stages exhibit good visual mimicry and/or have also developed an excellent flight response when coming into close contact with their ant model when it moves towards the bug while searching for EFNs on a host plant. The aggressive response of *Cr. subnuda* on encountering *R. linearis* is of potential ecological significance in terms of managing this pod-sucking pest in agro-ecosystems.

The behavioural responses of ants on encountering *R. linearis* ranged from neutral to aggressive while those of various instars of the bug ranged from neutral to submissive towards both its ant model and the non-model ant. However, all of the three nymphal instars displayed a significantly high avoidance response towards the model ant than the non model ant. The high tendency of avoiding their ant model suggests that the nymphs avoid close proximity to the ant model and tend to maintain a safe distance from them. This finding is in accordance with previous studies and confirms that the myrmecomorphs do not associate too closely with their models, and often avoid contact with them (Oliveira, 1985, 1988). In the majority of encounters with both species of ants the adult bugs chose to remain still and very often did not react at all to an approaching ant. All stages of the bug tested showed a tendency to flee from both species of ant, with the first instar exhibiting the highest and adult the lowest flight response. This may be due to the fact that the more vulnerable nymphal instars became progressively more submissive towards ants and as they developed into the relatively larger and less vulnerable fifth instar and adult. There was no significant difference between the flight response displayed towards its model, *Ca. compressus,* and that towards the non-model *Cr. subnuda*. In an earlier long-term field study the occurrence and abundance of the ant model, *Ca. compressus*, at extrafloral nectary's on hemipteran-harbouring plants (i.e. ant-preferred plants) was significantly higher than that of the other four co-existing species of ants, including *Cr. subnuda* (Kumari & Rastogi, 2018). It is plausible that the ant model has adapted to its mimic, which co-occurs on some of ant-visited plants and hence shows less aggression, particularly towards the tiny myrmecomorphic, first instar nymphs of the bug. It is reported that the myrmecomorphs that do not attack ants are almost always found in the same microhabitat as their models (McIver & Stonedahl, 1987). The results of our study show that though the vulnerable stages of the pod-sucking bug preferentially occur on pod-bearing plants frequently visited by their ant model, *Ca. compressus* (Kumari & Rastogi, 2018), probably to avoid predation while feeding as they do not offer any sort of resistance towards the ants. They simply avoid the ants while maintaining a safe distance from them.

This study provides an insight into the behavioural interactions between the myrmecomorphic *R. linearis*, its model, *Ca. compressus* and non-model, *Cr. subnuda* ants. It is interesting to note that though both ants were predominantly hostile towards the non-myrmecomorphic adult of the bug, the ant model *Ca. compressus* did not ever intimidate the first instar nymphs. Although it sometimes touched them with its antennae it mostly ignored them. Similarly, the ant model often ignored third and fifth instar nymphs, although occasionally it touched them with its antennae and rarely bites them. The non-model ant, *Cr. subnuda,* was consistently significantly more aggressive towards both the nymphs and adults of *R. linearis*. *R. linearis* bugs never exhibited any type of aggressive behaviour towards either of the ants. These ant-bug interactions have significant implications for the management of the pod-sucking bug as these ants could play a significant role in harassing this notorious pest of legumes.

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