Can a common and abundant plant-visiting ant species serve as a model for nine sympatric ant-mimicking arthropod species?

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Many arthropods mimic ants to avoid predation risk from visual predators. Our study of ant-mimicking arthropod diversity revealed 10 sympatric myrmecomorphs including spiders, mantids, bugs and grasshoppers. All, except one, were found predominantly on extrafloral nectary-bearing and homopteran harbouring plants. Of the five plant-visiting ant species, *Camponotus compressus*, *Camponotus paria*, *Camponotus sericeus*, *Crematogaster subnuda* and *Tapinoma melanocephalum*, only *C. compressus* showed significantly high occurrence and abundance on these plants. Except for a small spider morph, the remaining nine myrmecomorphic species resembled *C. compressus* and apparently use this common and abundant ant species as their model.

Keywords: Batesian mimicry, *Camponotus compressus*, herbivorous myrmecomorphs, *Myrmarachne* spp.

MYRMECOMORPHY (ant mimicry) is widespread among arthropods, particularly in the tropics[1–4], where ants are the dominant arthropods[5]. Ants exhibit high diversity, occupy a wide variety of habitats and are armed with protective devices such as poison-injecting sting, strong biting mandibles, defensive chemicals and ability to recruit colony members to attack intruders or predators[5]. Hence, with very few exceptions most predators are aversve to ants[6]. A large number of myrmecomorphic arthropods exhibit deceptive signalling or Batesian mimicry in which the unpalatable prey individual resembles a sympatric ant model to avoid attack by visually hunting predators[4,7,8].

Studies on the diversity of co-existing myrmecomorphs occurring in a local area are scanty[9]. A majority of studies have focused on the behaviour of individual species and most are on spider myrmecomorphs[4]. Myrmecomorphy is reported in >2000 arthropods[10]. It is most frequently reported in predatory arthropods such as spiders (including 43 spider genera, with 14 within the family Salticidae itself) and less commonly in mantids and phytophagous arthropods such as beetles, flies and plant bugs[1,11,12]. Ant models investigated in the tropics till now, belong most commonly to arboreal ant genera such as *Oecophylla*, *Camponotus*, *Crematogaster*, *Polyrachis* and *Tetraponera*[4,13]. The objective of our study was to examine the diversity of plant-visiting myrmecomorphs and ant species co-existing within a local area, in a tropical region. We hypothesize that the ant species with the highest occurrence and abundance on plants should be preferentially selected as the model by the majority of sympatric arthropod myrmecomorphs occurring on the same plants either as herbivores or as predators.

The present study was conducted in the ayurvedic and botanical gardens (with about 250 and 300 plant species respectively) of Banaras Hindu University, in Varanasi (25°18′N, 83°01′E), UP in India.

A field survey was carried out to record the occurrence (no. of plants visited by a particular species) and abundance (no. of individuals/plant) of plant-visiting ant species on three types of plants: (i) extrafloral nectary-bearing plants (EFN plants, hereafter), (ii) homopteran-harbouring plants and (iii) control plants. The plant preference and abundance patterns were determined for the plant-visiting myrmecomorphic species. Extrafloral nectaries are glands located anywhere on a plant except at the sites involved in pollination. These glands produce an aqueous solution containing sugars and other compounds[14] which attract a variety of plant-visiting ant species. Homopterans occur as sap-feeding herbivores on many plant species and they provide honeydew to the tending worker ants[15]. Control plants included those plants which lacked EFNs and did not harbour homopterans at any time during the observation period. Each plant was visually scanned (5 min/plant), taking care not to disturb the associated arthropods. All observations were made during the morning hours, from 8:00 h to 11:00 h, 4 times/month, from June 2010 to May 2011. The plant-visiting ant species and myrmecomorphs were collected live, brought to the laboratory and transferred to 75% alcohol for later identification by experts. The area near the nest ($n = 15$, in each case) of each plant-visiting ant species was monitored for the occurrence of myrmecomorphs. Photographs were taken (Canon, 7D SLR) and the size of each ant and myrmecomorphic species was determined with the help of image analysis software (Image J).

The variations in abundance and occurrence of ant species and myrmecomorphs on each of the three plant categories were analysed using one-way ANOVA followed by Dunnett's *post-hoc* test. All data calculated in the form of proportion or percentage was arcsine transformed prior to statistical analyses. Statistical software SPSS-16 was used.

Myrmecomorphs were found on 15 plant species belonging to 8 families. These included the homopteran-harbouring plants: Solanaceae (2), Fabaceae (2), Bignoniaceae (2), Malvaceae (1) and Asclepidaceae (1); EFN plants: Bignoniaceae (1), Malvaceae (1), Euphorbiaceae (1); and the control plants: Lamiaceae (1), Euphorbiaceae (1), Rutaceae (1) and Asclepidaceae (1).

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Five ant species, viz. *Camponotus compressus*, *Camponotus paria*, *Camponotus sericeus* (Formicinae) *Crematogaster subnuda* (hereafter referred to as *Cr. subnuda*; Myrmicinae) and *Tapinoma melanocephalum* (Dolichoderinae) were recorded on the plants. The minor caste workers of *C. compressus* (6.696 ± 0.26 mm), *C. paria* (5.88 ± 0.04 mm) and *C. sericeus* (5.94 ± 0.05 mm) were of large size; those of *Cr. subnuda* were of medium size (2.72 ± 0.09 mm) and *T. melanocephalum* ants were of small size (1.42 ± 0.06 mm).

A total of 10 sympatric myrmecomorphic species, belonging to 7 genera and 4 arthropod orders were recorded on the ant-visited plants (Figure 1). These included four species of spiders, viz. *Myrmarachne plataleoides*, *Myrmarachne bengalensis*, *Myrmarachne orientalis*, *Myrmarachne* sp. (Araneae), two species of mantids: *Euantissa pulchra*, *Hestiasula brunneriana* (Mantodea), two species of bugs: *Riptortus linearis*, and *Sohenus uvarovi* (Hemiptera) and a grasshopper: *Letana megastridula* (Orthroptera). Another spider morph, *Castianeira flavipes* was recorded on the ground, within a distance of 15–20 cm, of *C. compressus* nest.

All the five spider mimics were recorded throughout the year although *C. flavipes* and *Myrmarachne* sp. were rarely found. The mantid, *E. pulchra* was not observed during peak summer (May–June) and winter (December–January) seasons. The bug mimics, *R. linearis* and *S. uvarovi* (respectively found only on *Uraria picta* and *Withania somnifera* plants); the grasshopper, *L. megastridula* and the mantid morph, *H. brunneriana*, were found only during the rainy season.

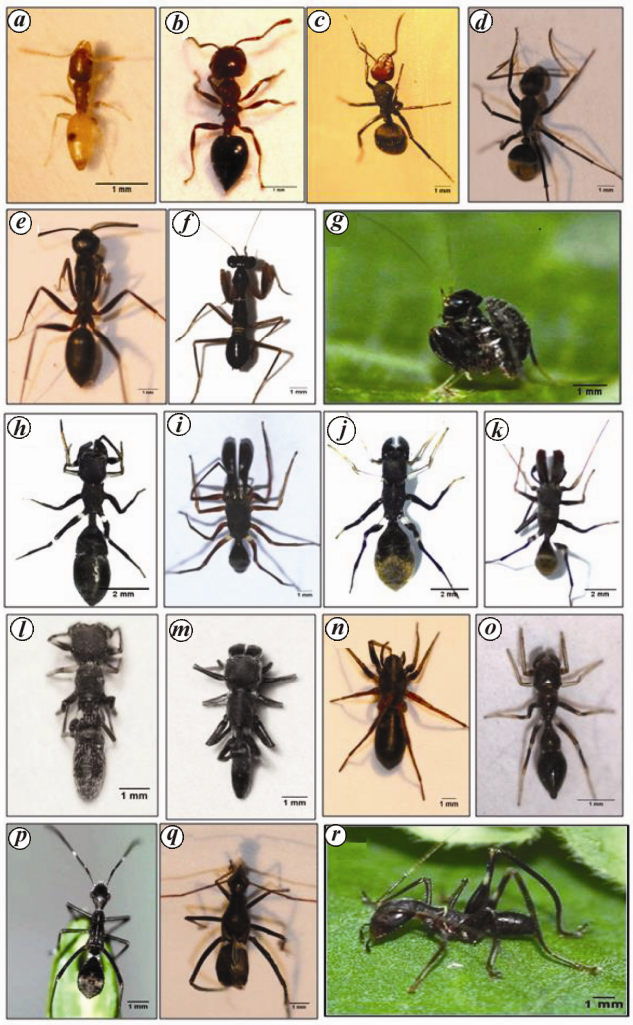

Figure 1. The 5 co-existing plant-visiting ant species: (***a***) *Tapinoma melanocephalum*; (***b***) *Crematogaster subnuda*; (***c***) *Camponotus sericeus*; (***d***) *Camponotus paria*; (***e***) *Camponotus compressus*, and the 10 co-existing myrmecomorphic species: the mantids: (***f***) *Euantissa pulchra*, and (***g***) *Hestiasula brunneriana*; Spider myrmecomorphs: *Myrmarachne plataleoides* (***h***) female and (i) male; *Myrmarachne bengalensis* (***j***) female and (***k***) male; *Myrmarachne orientalis* (***l***) female and (***m***) male; (***n***) *Castianeira flavipes*; (***o***) *Myrmarachne* sp.; hemipteran myrmecomorphs: (***p***) *Riptortus linearis* and (***q***) *Sohenus uvarovi*; (***r***) Orthopteran myrmecomorph: *Letana megastridula,* found in Banaras Hindu University campus, Varanasi, India (June 2010–May 2011).

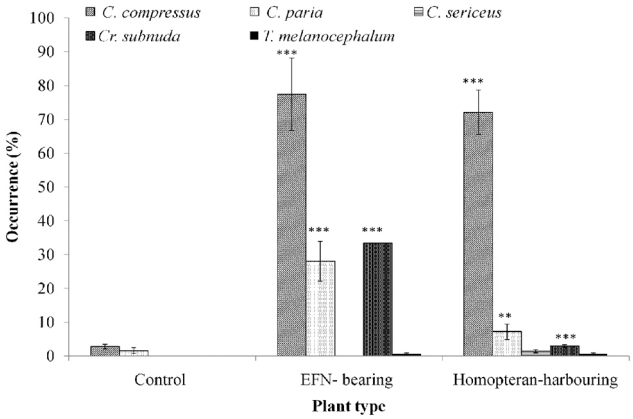

Figure 2. The occurrence (mean ± SE) of the 5 plant-visiting ant species on the 3 types of plants occurring in Banaras Hindu University campus, Varanasi, India, (June 2010–May 2011) (One way ANOVA, Dunnett's post-hoc test, $^{**}P < 0.01$; $^{***}P < 0.001$).

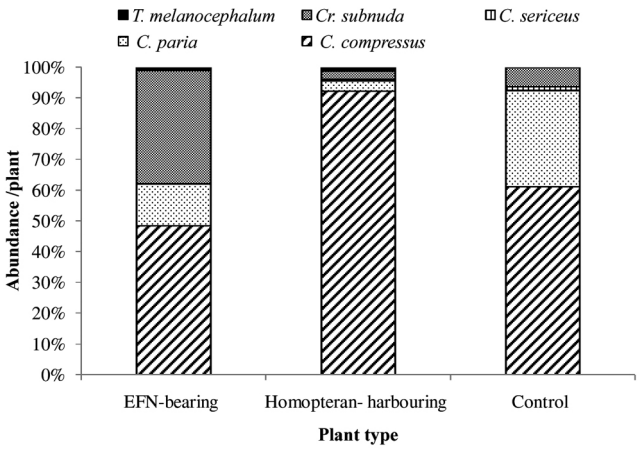

Figure 3. The abundance of the 5 plant-visiting ant species on the 3 types of plants occurring in Banaras Hindu University campus, Varanasi, India (June 2010–May 2011).

Table 1. Body length (mean ± SE), life cycle stage and feeding guilds of the 10 ant-mimicking myrmecomorphic species recorded on ant-visited plants, in Banaras Hindu University campus, Varanasi, India (June 2010–May 2011)

Myrmecomorph	Body length (mm)	Life cycle stage of mimic	Feeding guild	Order: family
Myrmarachne plataleoides	Male: 8.91 ± 0.54 Female: 6.81 ± 0.18	Mature	Predator	Araneae: Salticidae
Myrmarachne bengalensis	Male: 9.07 ± 0.28 Female: 6.78 ± 1.72	Mature	Predator	
Myrmarachne orientalis	Male: 9.05 ± 0.2 Female: 6.48 ± 0.69	Mature	Predator	
Myrmarachne sp.	2.74 ± 0.03	Mature	Predator	
Castianeira flavipes	7.13 ± 0.14	Mature	Predator	Araneae: Corinnidae
Euantissa pulchra	7.07 ± 0.14	I nymphal instars	Predator	Mantodea: Hymenopo didae
Hestiasula brunneriana	6.92 ± 0.07	I nymphal instars	Predator	
Riptortus linearis	6.19 ± 0.04	II and III nymphal instars	Herbivore	Hemiptera: Alydidae
Sohenus uvarovi	6.11 ± 0.13	Mature	Herbivore	Hemiptera: Miridae
Letana megastridula	6.25 ± 0.13	I nymphal instars	Herbivore	Orthoptera: Tettigoniidae

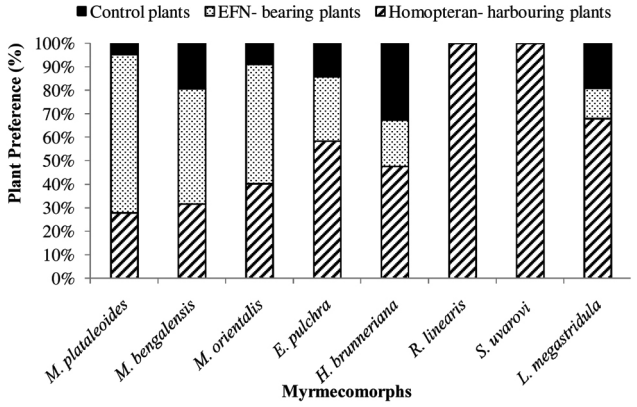

Figure 4. Plant preferences of the eight common myrmecomorphic arthropod species on the three types of plants occurring in Banaras Hindu University campus, Varanasi, India (June 2010–May 2011).

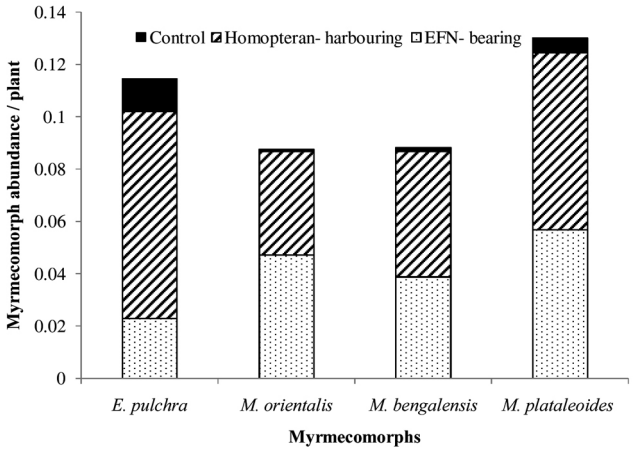

Figure 5. The abundance of the four most common morphs: *E. pulchra* and three species of spiders: *M. plataleoides*, *M. bengalensis* and *M. orientalis*, on the three types of plants occurring in Banaras Hindu University campus, Varanasi, Indias (June 2010–May 2011).

While male spiders were consistently larger, female spiders were similar, and hemipteran and orthopteran nymphal stage mimics were slightly smaller in size than *C. compressus* minor caste ants. The tiny spider, *Myrmarachne* sp. was much smaller than *C. compressus* ants and resembled *Cr. subnuda* in shape and size (Table 1 and Figure 1).

Out of five ant species, only *C. compressus* demonstrated a consistently higher ($P < 0.001$, in each case) occurrence and abundance patterns on each of the three categories of plants when compared to the co-visiting ant species. However, no significant differences were found between *C. compressus* and *C. paria* in terms of their occurrence and abundance on the control plants. While the occurrence of *C. compressus*, *C. paria* and *Cr. subnuda* was higher ($P < 0.001$, in each case) on the homopteran-harbouring and EFN plants, the abundance of each of these three ant species was higher on EFN plants ($P < 0.001$) when compared to control plants (Figure 2). Moreover, the abundance of *C. compressus* and *C. sericeus* was higher on homopteran-harbouring plants when compared to the control plants (Figure 3).

The preference of each of the three species of spiders, *M. plataleoides*, *M. bengalensis* and *M. orientalis* was significantly higher ($P < 0.001$, in each case) for EFN and homopteran-harbouring plants when compared to the control plants (Figure 4). Significantly higher ($P < 0.001$, in each case) preference patterns were shown by the mantids (*H. brunneriana* and *E. pulchra*), bugs (*R. linearis* and *S. uvarovi*) and grasshopper (*L. megastridula*) for the homopteran-harbouring plants when compared to the control plants. The abundance of the four most common morphs, *E. pulchra*, *M. plataleoides*, *M. bengalensis* and *M. orientalis* was significantly higher ($P < 0.001$, in each case) on EFN and homopteran-harbouring plants when compared to the control plants (Figure 5). Pearson correlation analysis revealed a positive correlation between the abundance of *C. compressus* and that of each of the four most common morphs on each of the three types of plants (except for the mantid morph on homopteran-harbouring plants) (Table 2).

Table 2. Pearson correlation coefficient between abundance of the plant-visiting *C. compressus* minor caste ants and the abundance of each of the four most common plant-visiting myrmecomorphic arthropod species: the mantid: *E. pulchra* and spiders: *M. plataleoides, M. bengalensis* and *M. orientalis*, on the three types of plants, occurring in Banaras Hindu University campus, Varanasi, India (June 2010–May 2011)

	Pearson correlation coefficient			
Plant type	*E. pulchra*	*M. plataleoides*	*M. bengalensis*	*M. orientalis*
Homopteran-harbouring	0.239	0.782	0.781	0.795
EFN-bearing	0.825	0.935	0.924	0.809
Control	0.606	0.729	0.583	0.713

The results reveal that *C. compressus* ants when compared to the four co-visiting ant species are not only higher in terms of their occurrence on the plants, but are also characterized by significantly higher abundance on both the homopteran-harbouring and EFN plants. It is well established that the abundance of mimics is usually several times lower than that of their models[6]. While the spider morphs preferred EFN plants, the mantid, hemipteran and the grasshopper myrmecomorphs preferred the homopteran-harbouring plants. Out of the 10 myrmecomorphs recorded in the study area, 9 species matched *C. compressus* in size, shape, relative occurrence and also abundance patterns. Hence, *C. compressus* fulfills the attributes of a suitable ant model for the sympatric arthropod myrmecomorphs. The only exception was the solitary *Myrmarachne* sp., which apparently used *Cr. subnuda* as its model. Our results also support earlier studies of the use of *Camponotus* spp. as a model by many spider mimics[16,17]. As Batesian mimics, both predatory and herbivorous plant-visiting myrmecomorphs would gain an advantage in avoiding predation by resembling *C. compressus*, the most abundant and commonly occurring ant species.

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