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Where there are ants, there are ant mimics: occurrence of jumping spiders that mimic ants on the castor plant across India

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Abstract. Ant mimicking jumping spiders of the genus *Myrmarachne* are common on castor plants (*Ricinus communis*) at ten different sites in India. Mimics of *Camponotus compressus* were the most common, perhaps due to the great abundance of their models on plants with extrafloral nectaries, and the similar size of these mimics. We also discuss the absence of the model ants at some of our sites, as well as the ecological significance of jumping spiders on castor plants.

Keywords. Batesian mimicry, Euphorbiaceae, extrafloral nectaries, parasites of mutualism, *Myrmarachne*, plant animal mutualism, plant defense against herbivory, *Ricinus communis*, Salticidae

The jumping spiders (Salticidae) constitute the most speciose family of spiders, comprised of 667 genera and over 6,000 species (World Spider Catalog, 2022). Apparent (or hypothetical) mimicry by many salticids, to include aggressive mimicry and Batesian mimicry of various other arthropod species, has been well documented (Edmunds, 1978; Jackson & Wilcox, 1990; Nelson & Jackson, 2009; Reiskind, 1977). Many salticids display *myrmecomorphy*, a morphological or behavioral resemblance to ants (Cushing, 1997; McIver & Stonedahl, 1993).

Myrmarachne (*sensu latu*) MacLeay, 1839 is one of at least 14 genera of ant mimicking spiders in the family Salticidae. This mimicry is most likely a form of Batesian mimicry wherein the spiders derive a survival advantage by resembling ants, which are considered unpalatable by many predators owing to their aggressive nature, strong mandibles, and sting (Reiskind, 1977). Spiders in the genus *Myrmarachne* have many morphological adaptations to enhance their resemblance to their ant models. Common modifications include constriction of the spider's two segmented body to resemble the three segmented body plan of the ant, the modification of chelicerae or pedipalps to resemble the mandibles of ants, and the use of the first or second pair of legs as antennae (McIver & Stonedhal, 1993). In addition to these morphological resemblances, they also show a number of behavioral adaptations, not seen in non-mimic salticids, apparently to mimic their ant models. These mimics cover similar distances and have similar trajectories as the ants in one round of continuous locomotion and tend to turn while moving (as opposed to turning while stationary, which is typical of other jumping spiders). Furthermore, the movement of these ant mimicking spiders is interspersed with very short (~100 ms) breaks during which they raise the first pair of legs to give the illusion of antennae (Nelson & Card, 2016; Shamble, 2017).

The aversion against ants by visual predators has been found to be successfully carried over to ant-mimicking spiders, despite the fact that spiders represent a significant portion of the predators' diet (Durkee et al., 2011, Nelson, 2012). Furthermore, some studies have shown that predators that have never seen ants avoid preying on ant-mimicking spiders, indicating that this aversion can be innate in some predators (Nelson et al., 2006; Huang et al., 2011). Ant-mimicking spiders are usually found in close proximity to their ant models. In some cases they can be found in the general vicinity of the foraging sites of their model ant, but interactions between them are limited because the spiders tend to avoid being present along the routes of the ants (Edmunds, 1978).

Especially in the tropics and subtropics, ants often congregate at the extrafloral nectaries (EFNs) of plants, which are simply nectaries found on plant parts other than flowers. Nectar from these structures attracts ants (or, less commonly, other arthropods) that attack or deter herbivores from the plant, representing a form of ant-plant mutualism. Ant-mimicking spiders may also be common on EFN-bearing plants due to the abundance of their ant models. Here, we studied one EFN-bearing plant, the castor plant *Ricinus communis* (Euphorbiaceae), which is a small to medium sized, soft, wooden plant that is widely distributed across the tropics. It is native to Ethiopia in Africa but was introduced as an oilseed to the Indian subcontinent thousands of years ago (Anjani, 2014). The castor bean plant produces EFNs at the base of petioles, on the leaf laminae, as well as on the peduncles of its imperfect flowers (Taylor et al., 2014), and attracts a variety of ant visitors.

We sampled ant-plant interactions and recorded observations of ant-mimicking spiders on castor plants at multiple sites in the Indian subcontinent between April and September 2022. We observed many ant-mimicking spiders belonging to the genus *Myrmarachne*, in addition to many ant species, visiting the EFNs of castor plants. Our working hypothesis for this study was that the most common ant mimic spider species at each site would be a mimic of the most abundant ant species at that site.

We sampled sites along a latitudinal gradient in India, covering seven states and ten sites (Table 1, Figure 1). These sites fall approximately in the central longitudinal region of India (Figure 1) and were selected because they had similar green cover, elevation above sea level, and extent of urbanization. We visited three different sites in Ramnagar (Ramnagar 1, 2, and 3, Table 2).

Table 1. Study sites, from north to south in India.

site		latitude, longitude
1	Ramnagar, Uttarakhand	29.32790°N, 79.05110°E
2	Aligarh, Uttar Pradesh	27.89420°N, 78.03500°E
3	Gwalior, Madhya Pradesh	26.22850°N, 78.26020°E
4	Bhopal, Madhya Pradesh	22.22310°N, 77.33860°E
5	Nagpur, Maharashtra	21.24960°N, 79.08410°E
6	Hyderabad, Telangana	17.33040°N, 78.43940°E
7	Hampi, Karnataka	15.33660°N, 76.46180°E
8	Bangalore, Karnataka	13.06630°N, 77.52240°E
9	Srirangam, Trichy, Tamil Nadu	10.86220°N, 78.69530°E
10	Kanyakumari, Tamil Nadu	8.08370°N, 77.52240°E

Field work took place between April and September 2022. Each of the 12 sites was searched for a thriving population of castor plants, and in every site, 10–20 plants were tagged for observation. Scan sampling was carried out on these plants for at least three consecutive days. The scans commenced at 0:800 and ended at 12:00, with an average interval of 20-minutes between each scan. During each scan,

all tagged plants were sequentially searched for arthropods. The presence of ant-mimicking spiders was also noted. The plants were inspected in a way that would cause little to no disturbance to the behavior of the visiting arthropods. Each observation of an ant mimicking spider (*Myrmarachne* sp.) was recorded with reference to the ant species it appeared to be mimicking. Photographs of the ant-mimicking spiders were taken whenever possible. Ant-mimicking spiders were identified by looking closely at their eyes, which were arranged in the typical salticid pattern, by observing their behavior, and by observing whether they jumped or made webs while descending. Some spiders were easy to identify because the quality of their mimicry was poor.

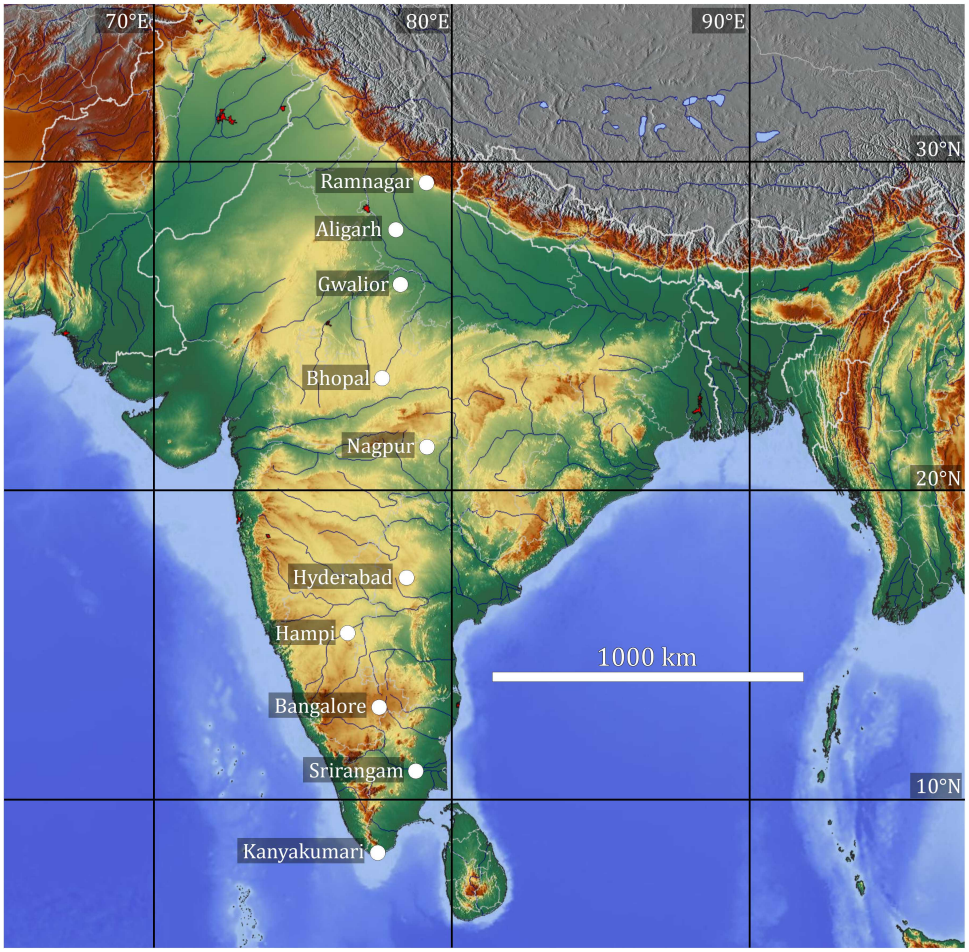

Figure 1. Study sites in India.

Across the ten sites, we observed *Myrmarachne* species mimicking at least seven different ant species (Table 2, Figure 2). In most instances (61.4% of observations), model ants were present on either the same plant or on one or more of the tagged plants in the site, whereas 36.4% of the time, model ants were absent. Most *Mymarachne* species were associated with common, widespread ant genera, especially *Camponotus*, *Polyrhachis*, *Crematogaster*, and *Tetraponera*, but the ant mimics we observed at any one site did not necessarily match the most abundant ant species that we found during at that site. For 45.5% of our records, the most common ant species that spiders appeared to mimic was *Camponotus compressus*, and *Myrmarachne kuwagata* was the most frequently observed spider species to associate with this ant. At 13.6% of observations, *Camponotus sericeus* was the second most common model, followed by *Crematogaster* sp., *Tetraponera rufonigra*, *Camponotus parius*, *Oecophylla smaragdina*, and *Meranoplus bicolor*.

Table 2. Incidence of ant mimic spiders on castor plants across the Indian subcontinent. The presence of model ant species was determined based on whether we saw that model ant species on any of the plants in the population that we sampled at each site. For the most abundant ant species, we omitted ant species that are typically much smaller in size than *Myrmarachne* sp. spiders to compare spider observations to ant species that they appear to mimic. Abundance data was not available for sites marked *NA*.

ant model	spider (if known)	spider count	site	model ant present?	most abundant ant
Crematogaster sp.	*Myrmarachne* sp.	1	Srirangam	no	*Camponotus irritans*
Crematogaster sp.	*Myrmarachne* sp.	1	Nagpur	no	*Camponotus compressus*
Crematogaster sp.	*Myrmarachne* sp.	2	Aligarh	no	*Camponotus compressus*
Crematogaster sp.	*Myrmarachne* sp.	1	Ramnagar 1	yes	*Crematogaster* sp.
Camponotus compressus, *Polyrhachis* sp.	*Myrmarachne kuwagata* Yaginuma, 1967	3	Nagpur	yes	*Camponotus compressus*
Camponotus compressus, *Polyrhachis* sp.	*Myrmarachne kuwagata*	1	Gwalior	yes	*Camponotus compressus*
Camponotus compressus, *Polyrhachis* sp.	*Myrmarachne kuwagata*	2	Aligarh	yes	*Camponotus compressus*
Camponotus compressus, *Polyrhachis* sp.	*Myrmarachne kuwagata*	1	Bangalore	yes	*Camponotus parius*
Camponotus compressus, *Polyrhachis* sp.	*Myrmarachne kuwagata*	2	Hampi	yes	*Polyrhachis* sp.
Camponotus compressus, *Polyrhachis* sp.	*Myrmarachne kuwagata*	2	Bhopal	yes	*Camponotus compressus*
Camponotus compressus, *Polyrhachis* sp.	*Myrmarachne kuwagata*	2	Ramnagar 1	yes	NA
Camponotus compressus, *Polyrhachis* sp.	*Myrmarachne kuwagata*	3	Ramnagar 2	yes	*Crematogaster* sp.
Camponotus compressus, *Polyrhachis* sp.	*Myrmarachne kuwagata*	4	Ramnagar 3	yes	NA
Camponotus sericeus	*Myrmarachne* sp.	1	Kanyakumari	yes	*Crematogaster* sp.
Camponotus sericeus	*Myrmarachne* sp.	1	Bangalore	no	*Camponotus parea*
Camponotus sericeus	*Myrmarachne* sp.	1	Hyderabad	yes	*Crematogaster* sp.
Camponotus sericeus	*Myrmarachne* sp.	1	Hampi	no	*Polyrhachis* sp.
Camponotus sericeus	*Myrmarachne* sp.	1	Bhopal	no	*Camponotus compressus*
Camponotus sericeus	*Myrmarachne* sp.	1	Srirangam	unknown	*Camponotus irritans*
Tetraponera rufonigra	*Myrmarachne melanocephala* MacLeay, 1839	1	Bangalore	no	*Camponotus parius*
Tetraponera rufonigra	*Myrmarachne melanocephala*	1	Hampi	no	*Polyrhachis* sp.
Tetraponera rufonigra	*Myrmarachne melanocephala*	1	Ramnagar 1	no	NA
Tetraponera rufonigra	*Myrmarachne melanocephala*	2	Pamnagar 2	no	*Crematogaster* sp.
Oecophylla smaragdina	*Myrmaplata plateleoides* (O. Pickard-Cambridge, 1869	2	Hampi	no	*Polyrhachis* sp.
Camponotus parius	*Myrmarachne* sp.	1	Ramnagar 1	yes	NA
Camponotus parius	*Myrmarachne* sp.	2	Ramnagar 3	yes	NA
Meranoplus bicolor	*Myrmarachne* sp.	1	Srirangam	yes	*Camponotus irritans*

We observed ant mimic spiders across the full latitudinal range where we sampled castor in India, from 29.3°N south to 8.1°N. We found ant mimicking spiders in each of the ten sites that we sampled, although we had too few data points to draw any conclusions on spider diversity. The *Myrmarachne* species we observed on the castor plant appear to be Batesian mimics of different ant species. Batesian mimicry is usually associated with a learned aversion to unpalatable prey by predators, which also benefits the palatable mimic (Uésugi, 1996). Moreover, for mimicry to be most effective, the number of models should be much higher than the number of mimics (Lindström et al., 1997). Ant-mimicking spiders are usually found in close proximity to their ant models (Edmunds, 1978), apparently to derive the full protective benefits of their mimicry. Thus the presence of ant-mimicking spiders on the castor plants, with their abundant ants, can be expected.

Camponotus compressus was the most common ant model in our study. This agrees with the observation that it frequents plants with extrafloral nectaries (Kumari & Rastogi, 2018). *Camponotus compressus* may also be a common model because these adult *Myrmarachne* spiders are similar in size. Ant-mimicking spiders may exhibit *transformational mimicry*, whereby they mimic different ant species during different stages of their lifecycle, corresponding to the model's size (Cushing, 1997). Therefore, it is possible that the spiders mimicking smaller ant species like *Crematogaster* sp. and *Meranoplus bicolor* were sub-adult instars.

In many cases, the apparent model ants were not observed at the same site as the mimics. There could be a number of explanations for the absence of our model ants (Table 3).

Table 3. Some possible explanations for the lack of model ants at a site frequented by their ant-mimics.

1	Ant models were missed during sampling; the model ant species may have been present on untagged plants in the same population.
2	Spiders do not always hunt where their models are found since ants are continuously relocating their nests to find favorable conditions with better resources and less competition (Smallwood, 1982).
3	There were temporal differences in the foraging period between the ants and the ant-mimicking spiders.
4	Innate (not learned) aversion in arthropod predators against ants and ant mimics has been documented before (Nelson & Jackson, 2006; Huang et al., 2011). Hence, it is possible that the ant mimicking spiders depend on the innate aversion of their ant model for protection rather than their physical presence.
5	At many of our sites, we observed the same spider on the same plant for days. Female spiders were commonly observed foraging in proximity to their nests on castor leaves (Figure 4). These observations suggest that spiders may be confined to certain plants even when their ant models are no longer present on them since they are nursing a developing brood of spiderlings.

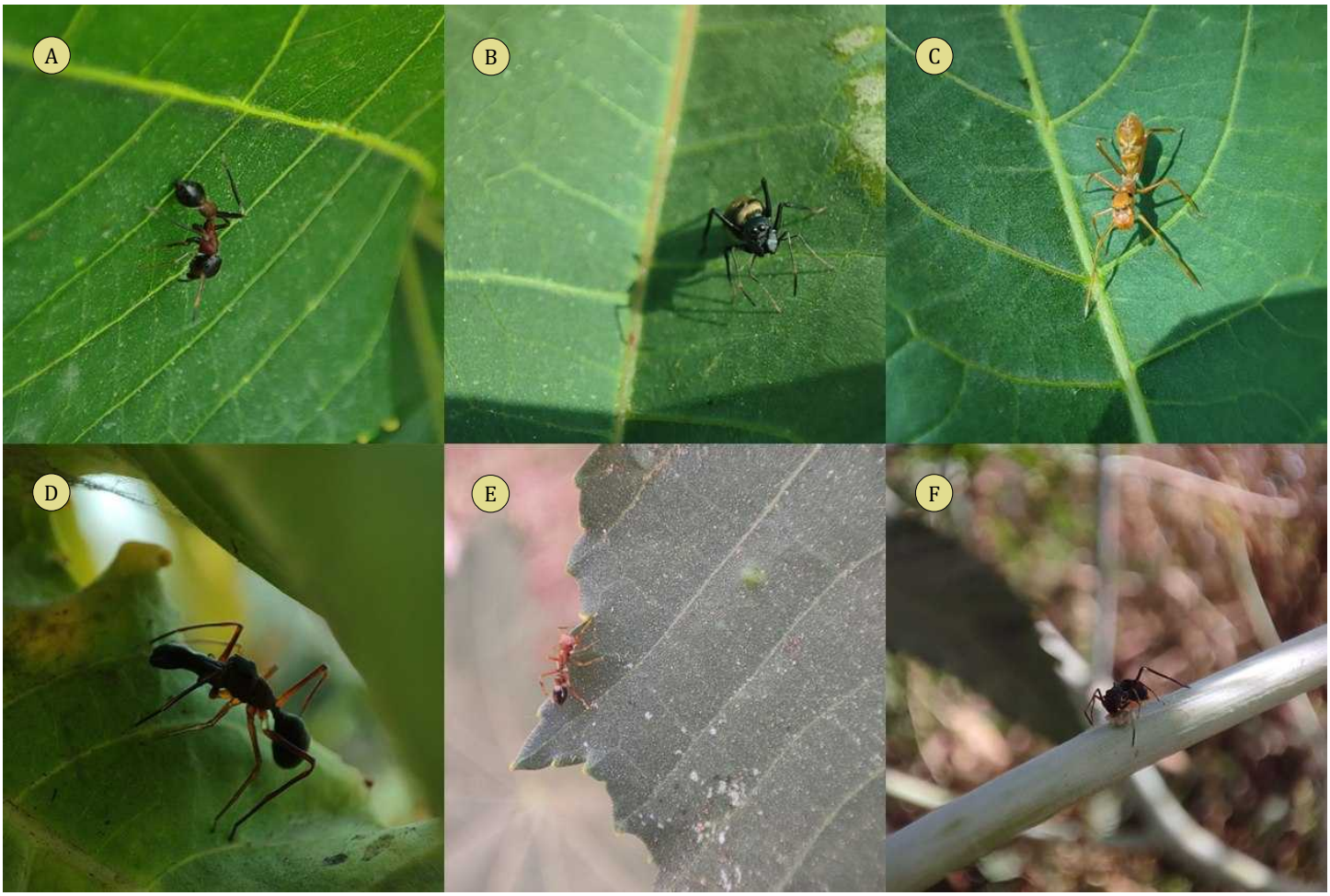

Figure 2. Ant-mimicking jumping spiders observed during our sampling of castor plants across India (associated ant species, or hypothetical models, in parentheses). **A,** *Myrmarachne melanocephala* female (*Tetraponera rufonigra*), Ramnagar. **B,** ♀ *Myrmarachne* sp. (*Camponotus sericeus*), Kanyakumari. **C,** ♀ *Myrmaplata plataleoides* (*Oecophylla smaragdina*), Hampi. **D,** ♂ *Myrmarachne kuwagata* (*Camponotus compressus*), Aligarh. **E,** ♀ *Myrmarachne* sp. (*Crematogaster* sp.), Srirangam. **F,** ♀ *Myrmarachne kuwagata* female drinking nectar from an extrafloral nectary on a castor plant, *Ricinus communis*, Gwalior. Photographs by Pooja Nathan.

In some instances (Figure 2F), we observed that the spiders were feeding on the extrafloral nectaries. Nectar feeding is common in salticid spiders (Jackson et al., 2001). Salticid spiders may be a yet unstudied mutualistic partner of EFN-producing plants, since they may also consume some of the plant's herbivores in addition to nectar from EFNs. We observed several different species of salticid spiders on castor plants in addition to spiders in the genus *Myrmarachne sensu latu* (Figure 3). These spiders may either prey on the ants, or feed at the EFNs. Our observations suggest that salticids are frequently associated with castor plants. The contributions of salticid spiders, especially those in the genus *Myrmarachne*, to the ecology and evolution of EFN producing plants such as the castor plant, have yet to be investigated and may serve as a useful system to study mimicry, mutualisms, and tritrophic interactions.

Figure 3. Non-mimicking salticids observed on castor plants. **A,** ♂ *Thyene imperialis* (Rossi, 1846). **B,** Immature *Carrhotus viduus* (C. L. Koch, 1846), a species known to associate with ants (Hill et al., 2021; Khalap & Hill, 2022). **C,** ♀ *Hyllus semicupreus* (Simon, 1885). **D,** *Madhyattus* sp.

Figure 4. ♀ *Myrmarachne kuwagata* in her nest on a castor leaf.

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References

Cushing, P. E. 1997. Myrmecomorphy and myrmecophily in spiders: a review. The Florida Entomologist 80 (2): 165–193.

Durkee, C. A, M. R. Weiss, and D. B. Uma. 2011. Ant mimicry lessens predation on a North American jumping spider by larger salticid spiders. Environmental Entomology, 40 (5): 1223–1231.

Edmunds, M. 1978. On the association between *Myrmarachne* spp. (Salticidae) and ants. Bulletin of the British Arachnological Society 4 (4): 149–160.

Hill, D. E., Abhijith A. P. C., Sanath R. M. and Harshith J. V. 2021. Ant associations of the jumping spider *Carrhotus viduus* in Karnataka, India (Araneae: Salticidae: Salticini). Peckhamia 249.1: 1-12.

Huang, J. N., R. C. Cheng, D. Li and M. Tso. 2011. Salticid predation as one potential driving force of ant mimicry in jumping spiders. Proceedings of the Royal Society B: Biological Sciences, 278 (1710): 1356–1364.

Jackson, R. R. and R. S. Wilcox. 1990. Aggressive mimicry, prey-specific predatory behaviour and predator-recognition in the predator-prey interactions of *Portia fimbriata* and *Euryattus* sp., jumping spiders from Queensland. Behavioral Ecology and Sociobiology 26: 111–119.

Jackson, R. R., S. D. Pollard, X. J. Nelson, G. B. Edwards and A. T. Barrion. 2001. Jumping spiders (Araneae: Salticidae) that feed on nectar. Journal of Zoology 255 (1): 25–29.

Kammili Anjani, K. A. 2014. A re-evaluation of castor (*Ricinus communis* L.) as a crop plant. CABI Reviews 9 (38): 1–21.

Khalap, R. and D. E. Hill. 2022. Use of a Green Tree Ant nest by the jumping spider *Carrhotus viduus* in Maharashtra, India (Araneae: Salticidae: Salticini). Peckhamia 257.1: 1-5.

Kumari, S. and N. Rastogi. 2018. Can a common and abundant plant-visiting ant species serve as a model for nine sympatric ant-mimicking arthropod species? Current Science, 2189–2192.

Lindström, L., R. V. Alatalo and J. Mappes. 1997. Imperfect Batesian mimicry - the effects of the frequency and the distastefulness of the model. Proceedings of the Royal Society of London B, Biological Sciences 264 (1379): 149–153.

Mclver, J. D. and G. Stonedahl. 1993. Myrmecomorphy: morphological and behavioral mimicry of ants. Annual Review of Entomology 38 (1): 351–377.

Nelson, X. J. , R. R. Jackson, D. Li, A. T. Barrion, and G. B. Edwards. 2006. Innate aversion to ants (Hymenoptera: Formicidae) and ant mimics: experimental findings from mantises (Mantodea). Biological Journal of the Linnean Society, 88 (1): 23–32.

Nelson, X. J. and R. R. Jackson. 2006. Vision-based innate aversion to ants and ant mimics. Behavioral Ecology, 17 (4): 676–681.

Nelson, X. J. and R. R. Jackson. 2009. Aggressive use of Batesian mimicry by an ant-like jumping spider. Biology Letters 5 (6): 755–757.

Nelson, X. J. 2012. A predator's perspective on the accuracy of ant mimicry in spiders. Psyche 2012 (168549): 1-5.

Nelson, X. J, and A. Card. 2016. Locomotory mimicry in ant-like spiders. Behavioral Ecology, 27 (3): 700–707.

Reiskind, J. 1977. Ant-mimicry in Panamanian clubionid and salticid spiders (Araneae: Clubionidae, Salticidae). Biotropica 9 (1): 1-8.

Shamble, P. S., R. R. Hoy, I. Cohen, and T. Beatus. 2017. Walking like an ant: a quantitative and experimental approach to understanding locomotor mimicry in the jumping spider *Myrmarachne formicaria*. Proceedings of the Royal Society B, Biological Sciences 284 (1858): 1-10.

Smallwood, J. 1982. The effect of shade and competition on emigration rate in the ant *Aphaenogaster rudis*. Ecology, 63 (1): 124–134.

Taylor, W., C. David and D. C. G. Victor. 2014. Insect visitation of peduncular and petiolar extrafloral nectar glands on castor bean (*Ricinus communis* L.) plants in Southern California. Journal of Evolutionary Biology Research, 6 (2): 5–8.

Uésugi, K. 1996. The adaptive significance of Batesian mimicry in the swallowtail butterfly, *Papilio polytes* (Insecta, Papilionidae): associative learning in a predator. Ethology 102 (5): 762–775.

World Spider Catalog. 2023. World Spider Catalog. Version 24. Natural History Museum Bern, *online at* http://wsc.nmbe.ch, accessed on 22 OCT 2022. doi: 10.24436/2