Aliens in the society: foreign arthropods and small vertebrates associated with the social spider Stegodyphus sarasinorum Karsch, 1892 (Araneae: Eresidae)

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Aliens in the society: foreign arthropods and small vertebrates associated with the social spider *Stegodyphus sarasinorum* Karsch, 1892 (Araneae: Eresidae)

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Abstract. Animals use nests for various functions including laying eggs, raising young and gaining protection from predators. Social insect colonies provide rich microhabitats for various foreign inhabitants. Social spiders in the family Eresidae live in large, long-lasting colonies with a dense silken nest where spiders reside in complex capture webs. Social spider colonies contain several organisms apart from the host spiders, yet little is known about the foreign species and their roles. In this study, we cataloged foreign animals found in the nests and webs of the Indian social spider *Stegodyphus sarasinorum* Karsch, 1892 from different sites in India. We then examined the abundance and diversity of foreign spiders in adult and juvenile colonies, and the nature of interaction of foreign spiders with host *S. sarasinorum* spiders. We found spiders classified into nine families and insects classified into five orders and a few small vertebrate taxa associated with *S. sarasinorum* colonies. Adult *S. sarasinorum* nests and webs contained significantly more foreign spiders than juvenile colonies. However, diversity of foreign spiders did not increase with the number of host spiders. Additionally, we found that foreign spiders found inside the nests preyed on individual *S. sarasinorum* spiders. Our study sheds light onto the intriguing biology of nest- and web-associates of social spiders.

Keywords: nest associates, commensals, web associates, *Philoponella*, social spiders

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Social insect nests are long-lasting, temperature- and humidity-controlled structures, endowed with rich resources such as brood, nest material or captured food (Parmentier 2020). Many social insect nests can be considered impenetrable homeostatic fortresses, as they are heavily guarded by an army of workers with potent stings and powerful bites (Hughes et al. 2008). Yet, several arthropods and small vertebrates use the nests to gain access to resources, and protection from predators and external environment. For example, termite mounds are used as fire refugia by short-snouted elephant shrew (Yarnell et al. 2008), for egg-laying by Andros iguanas (Knapp & Owens 2008), or to avoid thermal extremes by geckos (Vitt et al. 2007). Red wood ant colonies are used by numerous arthropods including wasps, beetles, flies, millipedes, centipedes, spiders, pseudoscorpions, mites and worms (Robinson & Robinson 2013). Mites, hive beetles and wax moths are serious pests and parasites of honey bee colonies (De Jong et al. 1982; Parmentier 2020). Considerable work has been done on the natural history of organisms associated with social insect societies (Cini et al. 2019; Parmentier 2020 and references within). These may be commensals, kleptobionts (organisms that steal food from hosts) or parasites. The association may be facultative or obligatory, and different life stages of insects (egg, larva, pupa, adult) may exploit the host colonies. They may employ behavioral, morphological or chemical adaptations to go undetected by the host (Breed et al. 2012; Cushing 2012).

Spiders are largely solitary, obligatory predators, but a handful of species (∼0.05%) are social (Agnarsson et al. 2006; Lubin & Bilde 2007; World Spider Catalog 2022). Similar to social insects, social spider colonies have long-lasting nests with multiple individuals. Social spider societies also seem to host various foreign arthropods and small vertebrates. In addition, nests are also a place where feeding takes place and food remnants can be found, and where spiders lay egg sacs. All these resources attract opportunistic foreign visitors to social spider nests. These characteristics make social spiders an ideal system to compare with the social insects. Unlike most social insects, social spider species are highly inbred (Lubin & Bilde 2007) and individuals within a colony are tolerant of conspecific individuals from other colonies, as well as other species (Kullmann 1972; Seibt & Wickler 1988; Lubin & Bilde 2007).

Foreign arthropods that have been reported inside the nests as well as on the webs of social spider species belong to Theridiidae, Eresidae, Desidae and Dictynidae (nest associates: Griswold & Meikle 1987; Downes 1994; Perkins et al 2007; Rao & Aceves-Aparicio 2012; Fernandez-Fournier & Avilés 2018; web associates: Lubin & Robinson 1982; Bradoo 1989; Cangialosi 1990; Downes 1994; Rypstra & Binford 1995; Leborgne et al. 2011; Straus & Aviles 2018). Although there are reports on foreign arthropods residing inside nests of *Stegodyphus* Simon, 1873 spiders (Bradoo 1972; Jackson 1987; Drisya-Mohan et al. 2019), few have examined the nature of interactions between these foreign associates and their social spider hosts.

Stegodyphus sarasinorum Karsch, 1892 (Eresidae), is a social spider found in semiarid habitats of India, Sri Lanka, Nepal and Myanmar. Tens of hundreds of individuals live in colonies where they collectively participate in hunting, web-building and brood care (Jambunathan 1905; Lubin & Bilde 2007). Each colony consists of a nest (lined with silk, leaves, twigs,

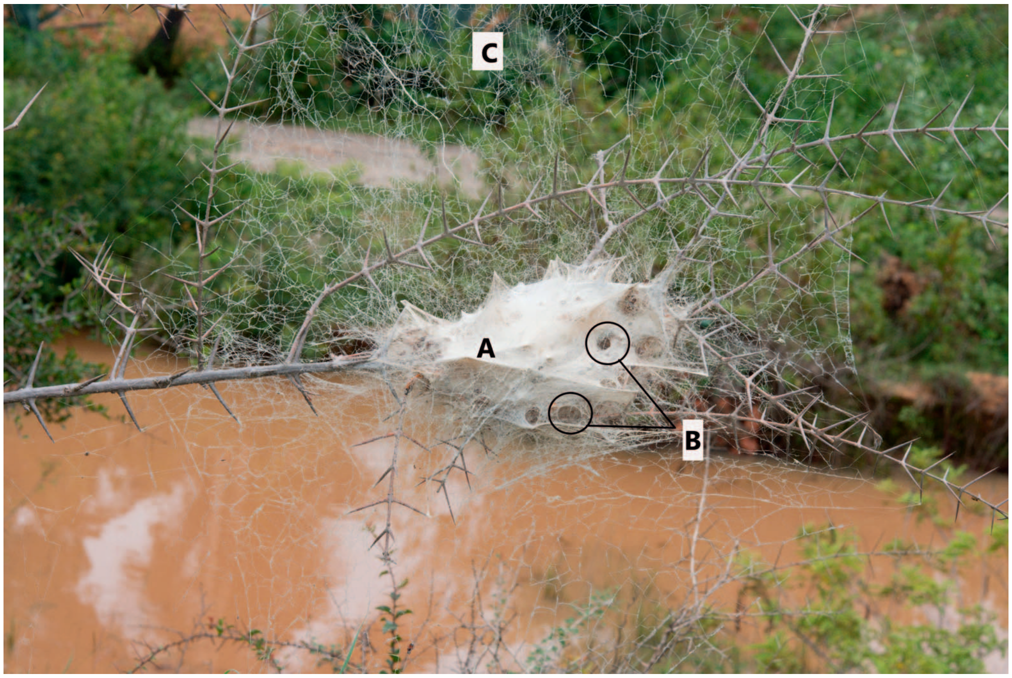

Figure 1.—*Stegodyphus sarasinorum* colony containing nest (A) white silken structure, nest entrances (B) through which resident spiders access interiors of the nest, and multi-dimensional sheet web (C) that is used to capture prey.

and debris), and a multi-dimensional, topologically complex web that is used to capture prey (Fig. 1). The nests are dense and protect spiders from direct sunlight and wind (Seibt & Wickler 1990; Crouch & Lubin 2000). *S. sarasinorum* colonies last for several months to a year, serving as a reliable resource that can be potentially utilized by other species. Early works of Bradoo (1972, 1989) and Jackson (1987) have reported some foreign arthropods in *S. sarasinorum* colonies. Potential interactions of these foreign associates could be commensal, kleptobiontic, parasitic, or predatory in nature. There is only one recent study that examines ants as potential kleptoparasites of *S. sarasinorum* (Drisya-Mohan et al. 2019). Detailed, systematic studies on foreign associates of *S. sarasinorum* colonies are lacking. Moreover, abundance, diversity, and the nature of interaction of foreign associates could vary with developmental stages of the host (*S. sarasinorum*) spiders. They could also incur a potential cost to host spiders where foreign associates can feed on the host spiders or affect their foraging abilities.

In this study, we (a) cataloged foreign arthropods and small vertebrates associated with *S. sarasinorum* colonies from various geographical locations, (b) examined the abundance and diversity of foreign spiders associated with juvenile and adult *S. sarasinorum* colonies and (c) conducted behavioral assays to explore the nature of interaction between foreign and host spiders. Our study highlights the need to examine these intriguing, lesser-known aspects of social spiders to understand factors contributing to sociality in spiders.

METHODS

Cataloging foreign associates of *S. sarasinorum*.—We sampled 70 adult, 61 juvenile, and 12 inactive *S. sarasinorum* colonies (where the host spiders had abandoned the nests) from several areas across states of India: Karnataka (13°4′52.04″N, 77°27′58.36″E; 12°44′9.11″N, 77°37′48.80″E; 12°53′12.07″N, 77°52′1.74″E; 12°51′32.90″N, 77°45′43.74″E), Andhra Pradesh (13°39′6.50″N, 78°27′24.11″E; 12°45′14.24″N, 78°20′12.48″E), Tamil Nadu (12°36′19.00″N, 78° 5′34.87″E) and Gujarat (22°27′43.35″N, 72°57′9.21″E; 22°31′39.21″N, 73°33′52.45″E; 22°16′46.36″N, 69°1′26.55″E) from January to March 2020, September 2020 to September 2021. We collected ten colonies at each sampling site. Once the colonies were visually located, we collected foreign spiders found on the web and preserved them for further identification. Social spider nests were brought back to Azim Premji University laboratory in Bangalore or to the nearest field station in Gujarat. The nests were then carefully opened to record the life stage (juvenile or sub-adult/adult) of the host spider based on their size (cephalothorax width and sexual maturity. Spiders that were less than 1.5 mm (cephalothorax width) were categorized as juveniles and larger than 1.5 mm were classified as sub-adults/adults. We measured around 15% of the juveniles, and 50% of the adults in any colony. We did not differentiate the later instar sub-adults from adults for the purpose of this study. All the foreign arthropods and small vertebrates found inside the nest were recorded. We conducted behavioral assays (see ‘host and foreign spider interactions’ section) with selected foreign spider families, and the rest were preserved in 70% ethanol for taxonomic identification. After sampling, social spiders were released back in the field. Voucher specimens of foreign spiders were deposited in Azim Premji University, Bangalore, India.

Abundance and diversity of foreign spider occurrence.—We counted the total number of foreign spiders present inside the nests and on the webs of adult and juvenile host colonies. Chi-square goodness of fit test was performed to examine the difference between adult and juvenile colonies.

Table 1.—Foreign spiders associated with *Stegodyphus sarasinorum* colonies.

Family	Genus/species	Web/nest associates
Uloboridae	*Philoponella feroka*	Web associates
	Philoponella sp.	
Theridiidae	*Argyrodes argentatus*	Web associates
	Rhomphaea sp.	
Salticidae	*Chrysilla* sp.	Nest associates
	Hyllus semicupreus (Simon, 1885)	
	Hyllus sp.	
	Icius alboterminus (Caleb, 2014)	
	Icius sp.	
	Madhyattus sp.	
	Menemerus sp.	
	Plexippus sp.	
	Rhene sp.	
Gnaphosidae	*Drassodes* sp.	Nest associates
	Poecilochroa sp.	
Sparassidae	*Olios lamarcki*	Nest associates
	Olios sp.	
Cheiracanthiidae	*Cheiracanthium* sp.	Nest associates
Thomisidae	*Indoxysticus* sp.	Nest associates
Lycosidae		Nest associates
Clubionidae	*Clubiona* sp.	Nest associates
Eresidae	*Stegodyphus tibialis*	Nest associates
Philodromidae	*Tibellus* sp.	Nest associates

We estimated the diversity of foreign spiders for each nest by calculating Shannon Wiener index, H=-$\sum p_i * l_{n(p_i)}$ where p_i is the proportion of the total sample represented by species i. We then examined the relationship between number of host spiders present in a nest and associated foreign spider diversity with a linear regression. All analysis was performed within R (R Core Team 2021)

Host and foreign spider interactions.—It was difficult to directly observe interactions between nest associates and host spiders as both reside inside the compact silken nests. Therefore, we decided to observe the nature of interactions in a lab-based behavioral assay. Foreign spiders from four families (Salticidae, Cheiracanthiidae, Gnaphosidae, and Sparassidae) that were predominantly found in *S. sarasinorum* nests were used for these assays. The foreign spiders were classified as adults based on their well-defined pedipalps and epigynum. Only adult foreign spiders were used for behavioral assays as they were found throughout the year in *S. sarasinorum* nests. A total of 38 trials were carried out. In each trial, we placed one host spider and one foreign spider collected from the same nest in a plastic Petri dish (8.5 cm diameter and 3 cm height) lined with tissue paper. The paper aided easier movement of the spiders as opposed to their movement on a glass base of the empty Petri dish. We noted if the foreign spider was larger or smaller with reference to the host spider. After initial acclimation, we observed them for two minutes. After this, spiders were left undisturbed overnight, and we observed them again the following day. Any predation event that occurred were recorded visually. In order to make the Petri dish trials to resemble natural habitat of these spiders, in a separate set of experiments (n = 10: Cheiracanthiidae and Gnaphosidae $n = 3$ each, Salticidae and Sparassidae $n = 2$ each), we provided retreat material inside the dish, and then observed any predation events.

Table 2.—Insects and vertebrate taxa associated with *Stegodyphus sarasinorum* colonies.

Class/Order	Taxon	Web/nest associates
Acari		Nest associates
Pseudoscorpiones		Nest associates
Lepidoptera	Microlepidoterans	Nest associates
Hymenoptera	Formicidae	Nest associates
	Vespidae	
Embioptera		Nest associates
Blattodea		Nest associates
Coleoptera		Nest associates
Reptiles	*Hemiphyllodactylus* sp.	Nest associates
Aves	*Leptocoma zeylonica*	Nest associates
Rodent	Muridae	Nest associates

RESULTS

Cataloging foreign arthropods associated with *S. sarasinorum*.—We found that 78.6% ($n = 70$) of adult and 62.3% ($n = 61$) of juvenile *S. sarasinorum* colonies had foreign arthropods associated with them. 83.3% ($n = 12$) of inactive colonies had foreign arthropod and vertebrate taxa. Arthropods including 19 foreign spider genera belonging to nine families, insects from five orders, Pseudoscorpiones, Acari and Vertebrates were also found in the nests (listed in Table 2, nest associates). Spiders of the families Theridiidae and Uloboridae were found exclusively on the web of the host (Table 1, web associates, Figs. 2 A,B). Some of the nest and web-associates are shown in Fig. 2.

Abundance and diversity of foreign spider occurrence.—Foreign spiders were significantly more abundant inside adult nests compared to juvenile nests ($\chi^2 = 11.36$, $P < 0.001$, df = 1). *Philoponella feroka* (Bradoo, 1979) was the most abundant species found on the webs (Fig. 2A). The number of web associates was significantly higher on adult webs compared to juvenile webs ($\chi^2 = 64.46$, $P < 0.0001$, df = 1).

There was no relationship between host numbers and foreign spider diversity associated within the nest (adult nests: $R^2 = 0.0002$, $n = 70$, $P = 0.904$; juvenile nests: $R^2 = 0.018$, $n = 61$, $P = 0.3$)

Host and foreign spider interactions.—We observed predation events in 71.0% of the trials. Foreign spiders predominantly preyed on host spiders in 63.15% trials. Predation by host spiders on foreign spiders was seen only in 7.9% of the trials. Some foreign spiders in the families Salticidae, Gnaphosidae and Sparassidae were always seen preying on host spiders. Cheiracanthiids were largely seen feeding on host spiders, except in three trials where host spiders fed on them (Fig. 3). Size range of host and foreign spiders were as follows: (Host spider $n = 38$, 3.92–8.94 mm), Salticidae ($n = 9$, 5.54–7.91 mm), Cheiracanthiidae ($n = 16$, 5.44–8.91mm), Gnaphosidae ($n = 7$, 5.87–9.31 mm) and Sparassidae ($n = 6$, 5.20–20.95 mm).

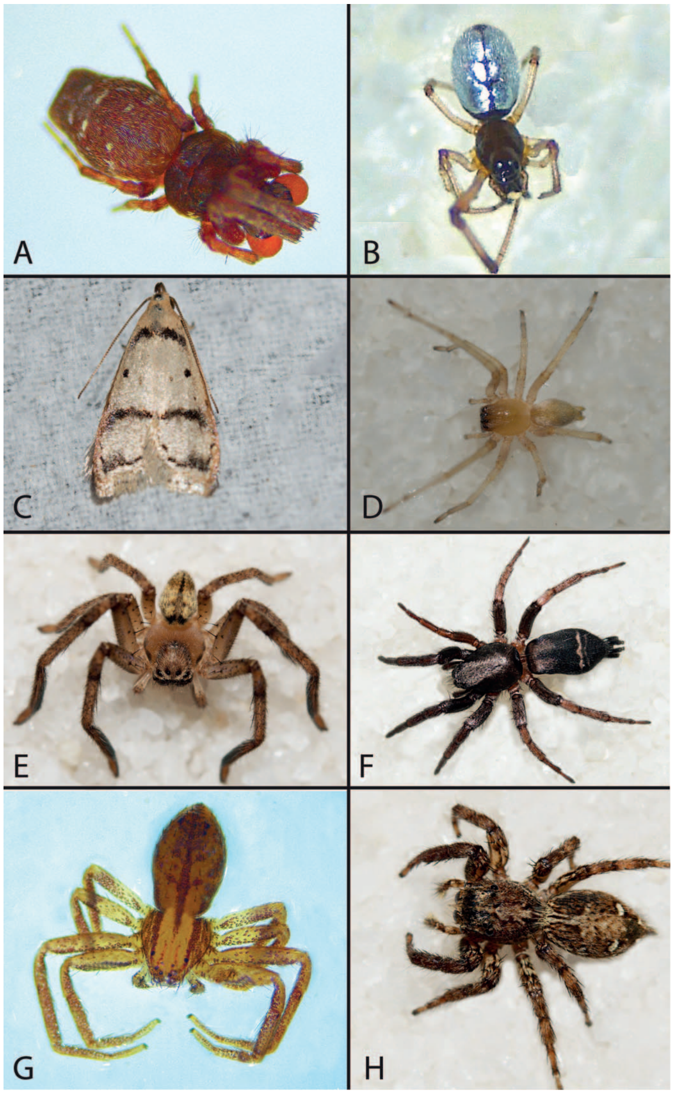

Figure 2.—A sample of foreign arthropods associated with *S. sarasinorum* colonies. A and B are web associates C–H are nest associates. A. *Philoponella feroka*, B. *Argyrodes argentatus*, C. Microlepidoptera, D. *Cheiracanthium* sp., E. *Olios* sp., F. *Poecilochroa* sp., G. *Tibellus* sp., H *Plexippus* sp. Images are not to scale.

In nine out of the ten trials, foreign spiders fed on host spiders even when the retreat material was present in the dishes. In these trials, foreign spiders were larger than host spiders.

DISCUSSION

Our results suggest that social spider *S. sarasinorum* nests serve as microhabitats, providing resources and shelter to various invertebrate and vertebrate communities. We retrieved spiders from nine families, insects from five orders, pseudoscorpions, mites, geckos, sunbirds and field mice from active nests. Inactive nests contained jumping spiders, sunbirds and geckos. Adult *S. sarasinorum* colonies had significantly more nest associates than juvenile colonies. These foreign associates used the nest for shelter, egg laying and opportunistically feeding on the host spiders or to consume prey remains.. Unlike the social insect colonies, social spider colonies are not endowed with rich resources like brood and stored food year-round. This perhaps limits the attraction of these colonies.

Some spiders in the family Uloboridae and Theridiidae shared the frames of their foraging webs with the webs of *S. sarasinorum*. The uloborid commensal spider, *Philoponella feroka* was more abundant than the theridiid kleptoparasite *Argyrodes argentatus* O. Pickard-Cambridge, 1880. Adult *S. sarasinorum* colonies also had significantly more web associates compared to juvenile webs.

Nest and web associates.—Foreign arthropods found inside social spider nests have been previously documented in various social spider families. Similar to the observations of Downes (1994), we noticed numerous visitors inside *S. sarasinorum* nests – these can be called opportunistic visitors as not all the nests that we sampled contained all of these arthropod species. We recorded 16 instances where foreign spiders in the families Salticidae, Cheiracanthiidae, Gnaphosidae and Sparassidae were seen with their own egg sacs and spiderlings inside *S. sarasinorum* nests.

Microlepidoptera (Fig. 2C) were found in 44.3% of the nests that we sampled. Various instars of the caterpillar, pupae and adult moths were seen, suggesting that they complete their life cycle inside the nests. In the lab, we saw the caterpillars feeding on *S. sarasinorum* nest material and debris. Bradoo (1972) reports caterpillars and moths from *S. sarasinorum* nests, but further examination of the specimens is needed to ascertain if these are the same species. Caterpillars and moths may employ various strategies to go undetected by *S. sarasinorum* individuals within a nest, and this needs further investigation.

Interestingly, we found a female individual of the sub-social spider *Stegodyphus tibialis* (O. Pickard-Cambridge, 1869) inside one of the nests. In the lab, *S. tibialis* was seen feeding on a prey along with *S. sarasinorum* individuals. Social spiders are not aggressive towards conspecific individuals from other colonies, as well as other species (Kullmann 1972; Seibt & Wickler 1988; Lubin & Bilde 2007).

On an average, two individuals of *P. feroka* were seen on *S. sarasinorum* webs. They were sometimes seen wrapping, and feeding on small prey caught on the host web. These spiders were either on host webs or on their own orb-webs, built between the gaps of *S. sarasinorum* webs. *P. feroka* have been reported as a commensal by Bradoo (1989). Whether they are strict commensals or compete with the juvenile host spiders remains to be tested.

Abundance and diversity of foreign spider occurrence.—We found that *S. sarasinorum* adult spider nests contained more foreign spiders compared to juvenile nests. Adult nests have larger nest entrances/openings (Fig. 1B), which the host spiders use to go in and out of the nest (pers. obs). Larger openings may provide greater access to the movement of foreign spiders. There was no relationship between the number host spiders inside a nest and diversity of foreign spiders. Rao & Aceves-Aparicio (2012) found that larger *Anelosimus baeza* Agnarsson, 2006 nests had more diverse foreign associates. They speculated that colony failures in the sub-social spider *A. baeza* are linked to a larger number of foreign inhabitants. We did not find this pattern in *S. sarasinorum* colonies.

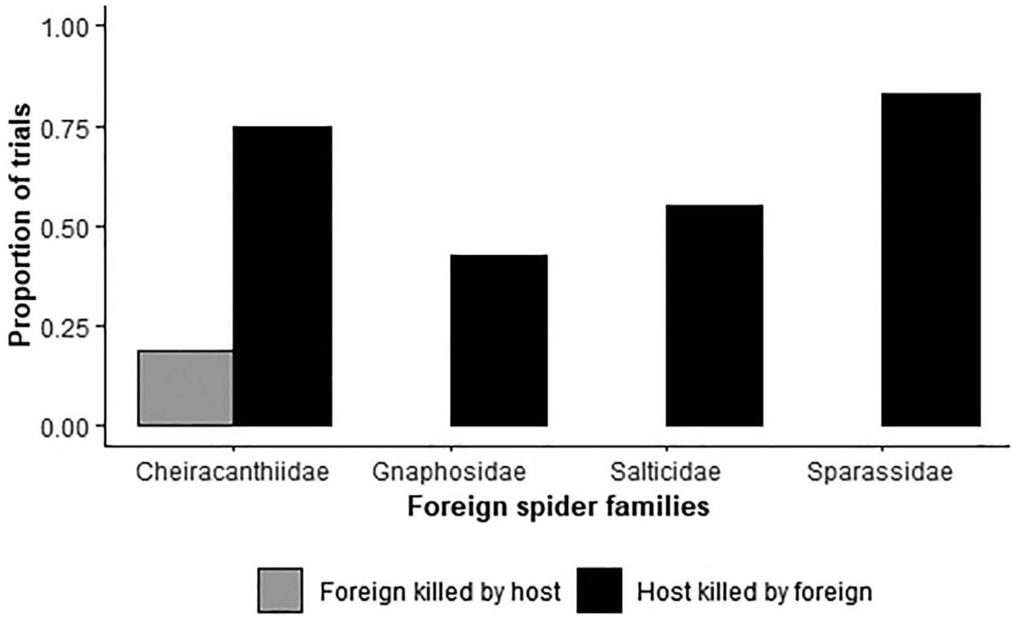

Figure 3.—Interaction between foreign and host spiders. Foreign spiders killed host spiders in most of the trails. *Foreign killed by host* represents the proportion of trials where foreign spiders were killed by host spiders. *Host killed by foreign* represents the proportion of trials where the host spiders were killed by foreign spiders.

Our study suggests that adult host webs also had more *P. feroka* compared to juvenile webs. Although there are no studies examining the abundance of commensals on *S. sarasinorum*, we can compare our results with other social spiders. Larger webs of *Anelosimus eximus* (Keyserling, 1884) harbored more kleptoparasites compared to *A. elegans* (Agnarsson, 2006), a sub-social spider (Straus & Aviles 2018). A greater number of commensal *Philoponella republicana* (Simon, 1891) was present on social spider webs compared to solitary spiders (Rypstra & Binford 1995). It is possible that adult *S. sarasinorum* webs provide commensals a greater area to forage compared to juvenile webs, however this needs to be tested. In addition, factors like seasonality and geographic distribution of commensals, nearby vegetation structure and presence of other web-building spiders are likely to influence the abundance of commensals on host webs.

Nature of interactions.—We noticed that foreign spiders attacked and consumed host spiders in most of the laboratory trials with or without the retreat material. In all these cases, foreign spiders were either larger or similar size as the host spiders. It is possible that foreign spiders had a size advantage over host spiders. Perkins et al. (2007) also found a similar trend in the social spider *Anelosimus studiosus* (Hentz, 1850) with its foreign spider associates. The retreat material of *S. sarasinorum* nests is much denser, making it difficult for spiders to move and interact with each other. Thus, in nature, such predation events may be rarer than our observations in the lab.

In summary, numerous foreign arthropods and occasional small vertebrate visitors utilize social spider nests and webs for multiple functions. While many may be transient visitors, some could be potential predators, commensals or parasites. Social spiders are considered successful because of their ability to collectively capture more prey (Lubin & Bilde 2007). Studies on social spiders worldwide have largely focused on hunting and web-building behaviors (Settepani et al. 2013; Modlmeier et al. 2014; Beleyur et al. 2015, 2021; Parthasarathy et al. 2019;). But the intriguing associates of social spiders merit further research to understand factors influencing sociality in spiders.

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