

Myrmecophily and kleptoparasitism of the weaver ant (*Oecophylla smaragdina*) by *Cosmophasis* cf. *bitaeniata* (Araneae: Salticidae: Chrysillini) in the Andaman Islands

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Abstract. This paper documents the behaviour of an unidentified jumping spider in the genus *Cosmophasis* (*C. cf. bitaeniata*) observed near leaf structures of the weaver ant *Oecophylla smaragdina*. These leaf structures were *pavilions*, woven together by the ants to protect trophobiotic hemipterans. The spider entered these pavilions and preyed on ant larvae and a hemipteran without eliciting an aggressive response from the worker ants. Retreat building in the wild by this *Cosmophasis* on an active foraging trail of *O. smaragdina* is also documented. Like *C. bitaeniata*, this spider appears to be a parasitic myrmecophile of *O. smaragdina* and it may use chemical mimicry to gain access to the pavilions of the host ant. Whether this *Cosmophasis* is a close relative or a subspecies of *C. bitaeniata* remains to be determined.

Introduction

Several species of spiders in the family Salticidae live in close association with ants. These associations have been classified into three functional groups: *myrmecomorphy*, *myrmecophagy* and *myrmecophily* (Cushing 2012). Myrmecomorphs like spiders in the genus *Myrmarachne* resemble the host ant species (Edmunds 1978). Myrmecophages like *Siler semiglaucus* (Simon 1901) prefer ants as prey (Jackson & van Olphen 1992). Myrmecophiles like the *Cosmophasis bitaeniata* (Keyserling 1882) do not visibly resemble or feed on their host ants but live alongside them (Allan & Elgar 2001).

Cosmophasis bitaeniata is distributed across Indonesia, New Guinea, Australia, Micronesia and Fiji (World Spider Catalog 2020) which is within the distribution of the tropical weaver ant *Oecophylla smaragdina* Fabricius 1775. *C. bitaeniata* has been found to live in close association with *O. smaragdina* by mimicking the cuticular hydrocarbon profile of the host ants. Studies have shown that *C. bitaeniata* does not biosynthesize this chemical profile but acquires a colony-specific hydrocarbon profile by consuming ant larvae (Allan et al. 2002). *O. smaragdina* are known to use chemical communication systems to establish territories, lay down foraging trails, trigger alarm systems against intruders and distinguish between nestmates and non-nestmates. They are highly territorial ants and respond aggressively to intruders or conspecifics from neighbouring colonies (Hölldobler 1983). By mimicking colony-specific cuticular hydrocarbons of *O. smaragdina*, *C. bitaeniata* are able to access these ant nests and steal larvae without eliciting an aggressive response from the host ants (Allan & Elgar 2001).

In addition to *O. smaragdina* larvae, *C. bitaeniata* have also been observed preying on hemipterans. Sap-sucking hemipterans release a carbohydrate rich honeydew that acts as a vital source of energy for large

O. smaragdina colonies (Blüthgen & Fiedler 2002). *O. smaragdina* are known to weave leaves together using larval silk and build leaf *pavilions*. These pavilions are primarily built to shelter hemipteran aggregation sites from adverse weather and potential threats from predators. It is important to note that pavilions are not used to raise the brood. Brood care takes place in *nests* (Blüthgen & Fiedler 2002). However, larvae are also present in pavilions during the construction process as larval silk is used to bind the leaves of the pavilion together.

Kleptoparasitic behaviour has been noted in two other genera within the Salticidae family Salticidae: *Simaetha* Thorell 1881 and *Portia* Karsch 1878. *Portia* have been observed feeding on prey stuck on the web of other spiders. A *Simaetha* species that lives inside the colonies of the social spider *Phryganoporus candidus* (L. Koch 1872) is known to glean insects from the webs of the host spider (Richman & Jackson 1992).

The weaver ant *Oecophylla smaragdina* is one of the most dominant life forms in tropical ecosystems where it is found. A single colony can grow as large as ~500,000 individuals that are actively scavenging, hunting and foraging (Lokkers 1990). This gives spider myrmecophiles like *Cosmophasis bitaeniata* an almost unlimited access to a food source in the form of ant larvae. Female *C. bitaeniata* are also known to build egg-sacs in or on the nests of these ants (Allan & Elgar 2001) providing a safe brooding site for the spider. The close association through chemical mimicry of *O. smaragdina* by *C. bitaeniata* has been well studied in Queensland, Australia (Allan & Elgar 2001; Allan et. al 2002; Elgar & Allan 2004, 2006). Even though both species have also been found in parts of Southeast Asia, no studies document this relationship outside of Australia. There are also no studies to date that document the behaviours associated with this relationship in their natural habitat.

This paper investigates the relationship between *O. smaragdina* and a *Cosmophasis* sp. indet. (cf. *bitaeniata*) in the Andaman Islands of India where this morphospecies of *Cosmophasis* Simon 1901 was frequently seen at a distance of less than 6 cm from weaver ant pavilions.

Location and habitat. The Andaman archipelago consists of 572 islands. The flora of these islands consists primarily of tropical evergreen, semi-evergreen, moist deciduous, littoral and mangrove forests. The study area was located on the northeastern shoreline of Havelock (Swarajdweep) Island and was subject to moderate to heavy winds during the study period as the Northeast monsoon brings rain and gusts to the Andaman Islands between the months of November and January. This study was conducted along the shoreline of a private plantation on Havelock (Swarajdweep) Island (Figure 1).

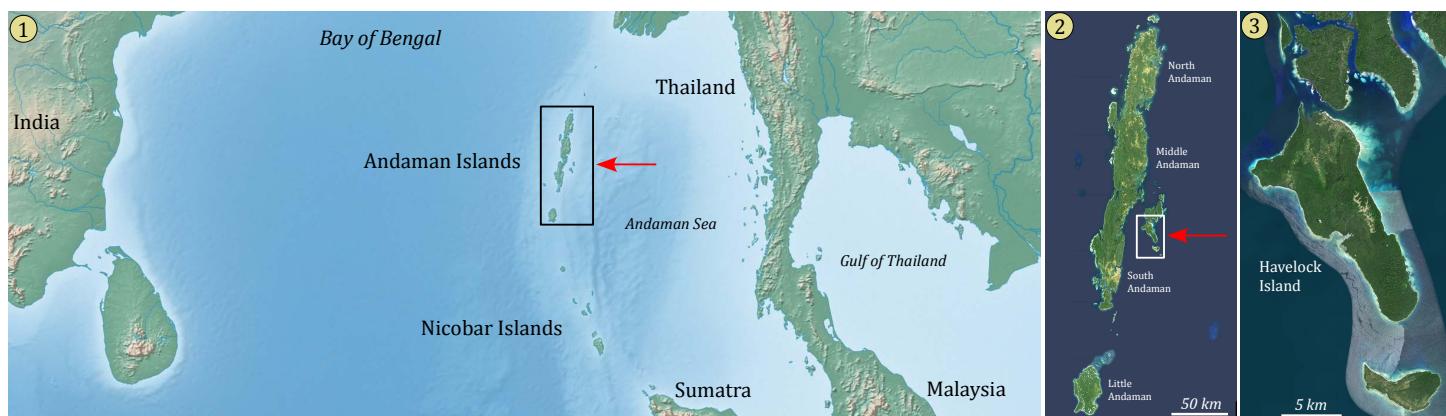


Figure 1. Location of Havelock (Swarajdweep) Island in the northeastern Indian Ocean. **1**, Location of Andaman Island archipelago in the northeastern Indian Ocean. **2**, Detail from inset (1) showing principal Andaman Islands (Landsat). **3**, Detail of inset (2) showing Havelock Island (Landsat).

Vegetation on this property was a mix of planted trees such as coconut, mango and areca palm alongside naturally occurring littoral vegetation that included *Thespesia populnea*, *Manilkara littoralis*, *Terminalia catappa*, *Gyrocarpus americanus* and *Guettarda speciosa*. Observations of ant-spider interactions near ant pavilions were primarily made in a low-lying patch of littoral vegetation that consisted entirely of *Thespesia populnea*. The base of all trees observed in this study began ~1-2 m inland from the intertidal zone. Branches with densely packed broad leaves stretched ~3-4 m into the intertidal zone. The outermost fringes of vegetation were found at a maximum height of ~3 m, with the height increasing gradually inland. The intertidal zone directly under the branches would be submerged in sea water as deep as ~1 m during high tide. During low tide, this patch was easily accessed with minimal disruption to the natural behaviour of the weaver ants and the *Cosmophasis* that were observed. Retreat building was observed on an *Areca catechu* tree that was ~100 m from the shoreline.

Observing behavioural interactions. To investigate the association between *Cosmophasis* cf. *bitaeniata* and *Oecophylla smaragdina* in this region, spiders and ants were observed when the spider was within ~6 cm of a weaver ant pavilion. All observations of spider-ant interactions near weaver ant pavilions were made in their natural environment during the month of NOV 2019. Observations were made between 12:00 and 16:00. On detecting a spider, behaviours were observed for 15-60 minutes. A total of 15 observations were made. Two observations of the *Cosmophasis* retreat building process were made on 2 MAY 2020 at 08:22 for 2 hours and at 16:17 for 5 minutes. A total of 28 daily observations were made from 3-30 MAY 2020 for ~5 minutes each.

Observations

Leaf structures constructed by weaver ants. The branches directly above the intertidal zone contained a high density of young green stems. These stems appeared to be the preferred aggregation site for the bugs (Hemiptera: Auchenorrhyncha) that mainly feed on tree sap. *Oecophylla smaragdina* built protective pavilions around these achenorrhynchan aggregation sites. Their pavilions were constructed 1.5-2.0 m above the ground. I also found a few abandoned sites suggesting that these leaf structures are ephemeral. Minor workers of *O. smaragdina* were seen tending to achenorrhynchans inside half-complete pavilions (Figure 2:1) while a large number of major workers were seen actively constructing the pavilion and patrolling the vicinity of the pavilion.

*Interactions between female *Cosmophasis* cf. *bitaeniata* and *O. smaragdina*.* In nearly all encounters, the spider was seen actively moving in and out of a pavilion of the host ant species. When I observed spiders that were moving towards a pavilion ~1 m distant, they appeared to use leaves and branches that were also used by major workers of the host ant as foraging trails.

In all 15 instances, inside the pavilion and on its periphery, these *Cosmophasis* were observed to move slowly and to stop briefly when it appeared to visually detect the presence of *O. smaragdina* major workers in its intended direction of movement. If the major workers continued to build leaf structures or to patrol with no apparent change in behaviour, the spider would continue along its path. One spider was also seen using leaf crevices to stop and seemed to make assessments of potential threat from major workers. These crevices appeared to be outside of the apparent line-of-sight of the major workers. These behaviours suggested that the spider was moving cautiously to avoid visual detection by major workers.

In a few encounters, a *Cosmophasis* walked within ~6 cm of *O. smaragdina* major workers and appeared to be in the apparent line-of-sight of a major worker. In these instances, the major worker appeared to fix its orientation towards the spider, wave its antennae and slowly move towards the spider. Antennation is typically a chemical assessment (Newey et. al 2010), in this case of a spider that visibly did not resemble an ant nestmate. The spider responded to this by turning to face the ant, waving its front pair of legs in the air, waving its pedipalps and slowly backing away from the ant. Raised front legs seems to be a common form of behavioural mimicry among spiders like *Siler semiglaucus* that live in close association with ants (Grob 2015). This behaviour presumably mimics antennation and creates the appearance of only three pairs of legs on the spider. While the exact purpose of waving the pedipalps is unclear, the chemosensitive hairs on their pedipalps (Foelix 1970) could facilitate the spider's chemical assessment of the ant. The spider disengaged from this behaviour when the major worker turned away from the spider, which was the outcome in all the cases.

All encounters in which the spider was visually detected by a major worker were limited to this apparent chemical assessment by the ant through antennation. When a *Cosmophasis* appeared to be within ~6 cm of minor workers and within the apparent line-of-sight of the ants, minor workers did not stop to assess them. There was no visible change in the behaviour of minor workers that were seen inside the pavilion.

Non-aggressive response towards female Cosmophasis cf. bitaeniata. by Oecophylla smaragdina. Non-nestmates other than this *Cosmophasis* coming within ~6 cm of the pavilions were met with an aggressive response by major workers. Wasps that landed too close to the pavilion incited major workers to move aggressively towards the wasp with raised gasters and flared mandibles. The same signs of aggression were directed at the observer when I got within ~12 cm of a major worker. Notably, I did not observe any other species of jumping spiders within 1 m of an *O. smaragdina* pavilion. I found at least one *Cosmophasis* within ~6 cm of an *O. smaragdina* pavilion during each of our 15 observations. Through the entire duration of our study, I did not observe any instances of aggression by major or minor workers of the colony towards one of these spiders.

Consumption of host ant larvae. *Oecophylla smaragdina* larvae were found in all leaf pavilions that were under construction and their silk was used by major workers to bind leaves together. The ant larva was plump, capsule-shaped and white with mild translucence. The larva was approximately half the body length (~ 1 cm) of the *Cosmophasis*. During one encounter, a female *Cosmophasis* was seen exiting an *O. smaragdina* pavilion with an ant larva held in its chelicerae. The spider appeared to move faster once it had picked up the larva. Unlike its slow approach on the way in, the spider was seen moving hastily away from the pavilion and the patrolling major workers. Away from the pavilion (8-10 cm away), the spider was seen holding the larva in its chelicerae and appeared to be consuming it.

Predation on auchenorrhynchans inside an ant pavilion. *Oecophylla smaragdina* appeared to consume the honeydew released by the trophobiotic auchenorrhynchans inside the pavilions. Major workers that left the pavilions and traveled further inland to other leaf structures were seen with expanded gasters, suggesting that they were carrying honeydew back to their nests (also noted by Blüthgen & Fiedler 2002). In one encounter I observed a female *Cosmophasis* snatching an auchenorrhynchan from inside a partially complete leaf enclosure. This spider navigated through a pavilion that contained multiple auchenorrhynchan aggregation sites, and ventured within ~1 cm of major workers but appeared to actively avoid visual detection by hiding in the crevices of small leaves. After snatching an auchenorrhynchan, the spider quickly exited the pavilion and jumped to an adjacent leaf (12-15 cm away) where it was seen feeding on it (Figure 2:2-3,5).



Figure 2. Interaction of female *Cosmophasis* cf. *bitaeniata* with weaver ants, *Oecophylla smaragdina*. **1**, Weaver ants tending to sap-sucking achenorrhynchans inside of a pavillion. **2**, This spider snatched an achenorrhychan that was tended by weaver ants several seconds previously. **3**, Spider moving away with the snatched insect. **4**, Spider watching weaver ants. **5**, Spider consuming the snatched insect.

Cosmophasis cf. bitaeniata building a retreat on an *Oecophylla smaragdina* foraging trail (Figure 3). A female *Cosmophasis* was observed around the splintered base of a branch on an *Areca catechu* tree. This site was within ~6 cm of an active weaver ant foraging trail where weaver ants were seen carrying insects towards nests in the canopy. The spider walked around within 15-20 cm of the splintered branch for over one hour before constructing several silk lines on the splinter. The spider appeared to be interrupted by major workers that came to the site to investigate the lines. When the major workers came within 1-2 cm of the spider, the spider was seen raising its front legs, waving its pedipalps and backing away from the workers. The spider returned to building the retreat when the major workers moved more away from the site. The first lines of silk were detected near 08:00 on 2 MAY 2020 and construction of the retreat appeared to be completed by 16:00 on the same day. The retreat was at a height of ~3 m from the ground.

I observed the retreat for 28 days after its construction. Weaver ants continued to use the foraging trail on the tree and appeared to stop and inspect the retreat at multiple times. After a brief inspection (10-30 seconds), the ants were seen returning to their foraging trail. 11 days after the retreat was constructed, another layer of silk was found covering the retreat. The process of construction of this additional layer of silk was not observed. From a visual assessment, this silk did not appear to be spider silk. It is important to note that during the observation period, I did not observe any other insects like caterpillars or spiders known to weave silk on this tree. At this juncture I hypothesise that the additional layer of silk could have been created by weaver ants after they detected the presence of colony-specific larval odours from the spider inside the retreat.

Discussion

Myrmecophily and chemical mimicry. Female *Cosmophasis cf. bitaeniata* were commonly found in and near (within ~6 cm) *Oecophylla smaragdina* leaf pavilions. They were observed retrieving and feeding on *O. smaragdina* larvae. The territorial aggression of *O. smaragdina* workers toward intruders and non-nestmates has been well documented (Newey et. al 2010). Studies have shown that *O. smaragdina* recognize some *Cosmophasis* species, to include *C. micans* (L. Koch 1880) and *C. micarioides* (L. Koch 1880) as intruders and respond with aggression (Allan & Elgar 2001). The apparent absence of any other salticids around the *O. smaragdina* pavilions observed in this study suggests that these areas may be hostile territories for other salticids. *O. smaragdina* major workers were observed turning towards *Cosmophasis cf. bitaeniata* to inspect the spider when it entered the ant's apparent line-of-sight. This suggests that major workers visually recognized these *Cosmophasis* as outsiders and responded with a chemical assessment of the spider by antennation. However, this did not lead to aggressive behaviours (raised gaster and flared mandibles) by the ants towards these spiders. This evidence suggests that, as with *C. bitaeniata* (Allan et al. 2002) the association between *Cosmophasis cf. bitaeniata* and *O. smaragdina* is based on chemical mimicry of the host ant by the spider and not morphology.

Kleptoparasitism. Honeydew gathered from their auchenorrhynchian partners is a vital food source that helps large arboreal ant-colonies to meet their high energy needs (Blüthgen & Fiedler 2002). *O. smaragdina* also invests energy in building leaf pavilions around auchenorrhynchian aggregation sites. These structures are built to protect the trophobiotic auchenorrhynchans from environmental influences and competitors; they act as *dairies* for large colonies that actively harvest honeydew from these trophobionts (Blüthgen & Fiedler 2002). My observations indicate that this *Cosmophasis cf. bitaeniata* is colony-parasitic, and *O. smaragdina* derives no apparent benefit from the association. It is interesting to note that the spider is not parasitising individual worker ants but the colony at large by stealing their larvae and the hemipterans that they harvest.

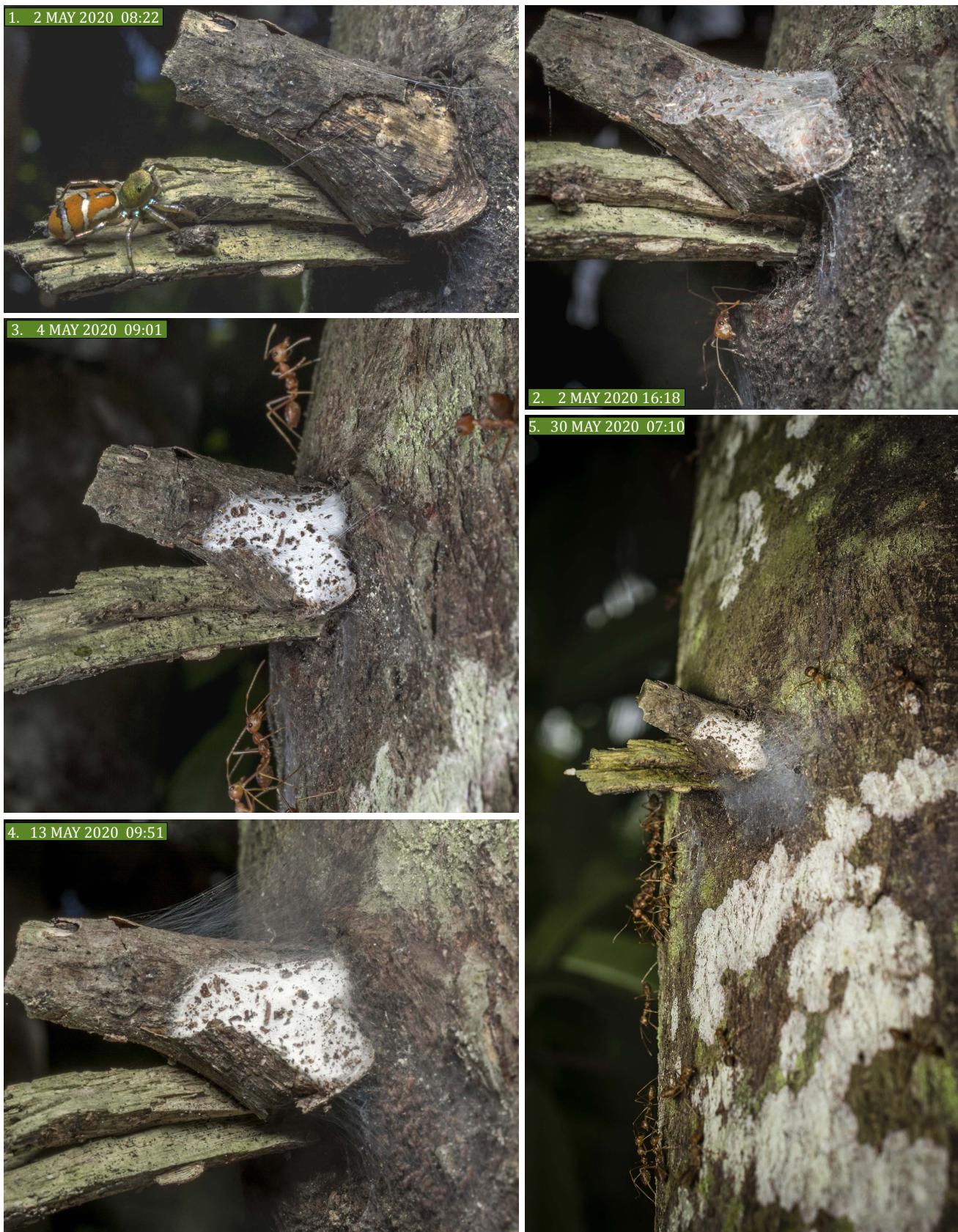


Figure 3. Female *Cosmophasis* cf. *bitaeniata* building a retreat on a foraging trail of the weaver ant *Oecophylla smaragdina*. **1**, The spider was beginning to construct a few silk lines. **2**, Retreat just before construction was fully completed (slight translucence). **3**, Weaver ants continued to use the foraging trail that passed less than ~6 cm from the retreat. **4**, Later the retreat was covered with an additional layer of silk that did not appear to be spider silk. **5**, After 28 days, weaver ants actively patrolled around the retreat and the structure remained intact.

A few studies have explored the possibility of mutually beneficial spider-ant associations. For example, Shepard and Gibson (1972) found that nests of the ant *Tapinoma melanocephalum* occupied by the jumping spider *Cotinusa* sp. appeared to be correlated with a higher brood to adult ratio than nests without spiders. The study proposed that this relationship could be considered mutualistic if the brood to adult ratio of each nest is used as an indicator of reproductive success. However, it is unknown if the diet of *Cotinusa* sp. includes larvae of the host ant and therefore unclear if the spider was choosing nests with a higher number of larvae. A study of *Cosmophasis bitaeniata* and *Oecophylla smaragdina* found a similar positive correlation between spider presence and the number of larvae in a nest. In the case of *Cosmophasis bitaeniata*, known to feed on ant larvae, this correlation might also suggest the spider is likely to target nests with more larvae (Allan & Elgar 2001), suggesting a colony-parasitic relationship.

O. smaragdina is a dominant ant species and plays a vital role in an ecosystem both as a top predator of arthropods and as a cryptic herbivore through the tending of achenorrhynchans (Philpott & Armbrecht 2006). One study found as many as six spiders living inside a single *O. smaragdina* nest and 36% of the nests surveyed were found to have a *Cosmophasis bitaeniata* in or on the nest (Allan & Elgar 2001). While the present study has uncovered the occurrence of kleptoparasitism and brood predation by *Cosmophasis* cf. *bitaeniata* living with *O. smaragdina*, a deeper understanding of the ecological distribution of both species in the Andaman Islands could highlight the role of kleptoparasitism and brood predation by this spider in regulating the populations of *O. smaragdina*. This warrants further investigation and could potentially uncover valuable insights into myrmecophily and its role in the functioning of ecosystems at large, as noted by Preston & Johnson (2010).

Based on its appearance and association with *O. smaragdina* colonies, the subject of this paper (*Cosmophasis* cf. *bitaeniata*) appears to be close relative, if not a northwestern subspecies, of *C. bitaeniata*. This relationship remains to be determined. The green scale cover of the carapace of female *C. cf. bitaeniata* from Havelock Island resembles that of *C. umbratica* Simon 1903, but the scale cover of the abdomen is close to that of *C. bitaeniata*.

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