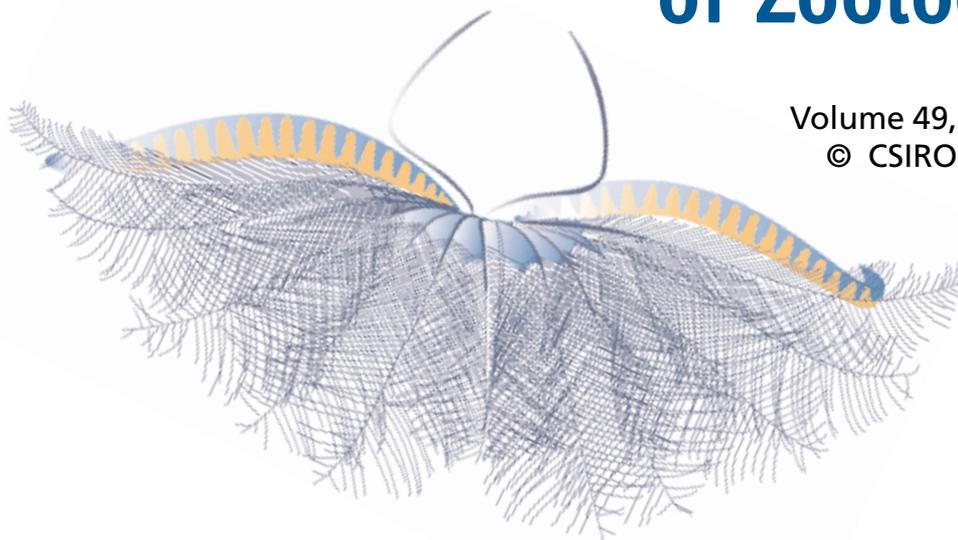


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## Exploitation of the green tree ant, *Oecophylla smaragdina*, by the salticid spider *Cosmophasis bitaeniata*

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### Abstract

The salticid spider *Cosmophasis bitaeniata* is a myrmecophilic associate of the green tree ant, *Oecophylla smaragdina*. The abundance of *C. bitaeniata* on a tree or shrub is positively correlated with the number of nests of *O. smaragdina* on that vegetation. Experiments with captive spiders confirmed that the spiders prey on the larvae of their highly territorial and aggressive ant host, typically by removing the larvae from the mandibles of minor workers. *C. bitaeniata* avoids direct contact with major workers of *O. smaragdina* in daylight, but congeners elicited higher activity levels of major workers than either nestmate workers or *C. bitaeniata*. These data suggest that *C. bitaeniata* may be an exploitative chemical mimic of its host.

### Introduction

A variety of insects and arachnids live in association with ants (Hölldobler and Wilson 1990; Elgar 1993; McIver and Stonedahl 1993 for reviews). Ant associates may be brood predators, mutualists, scavengers, endoparasites or commensals and are found in and around the nests of their host. For example, brood predators typically live within the brood chambers of the nest, pseudoscorpions live in the debris chambers, mites live on the bodies of workers and several species of Diptera follow their hosts' foraging trails (Hölldobler and Wilson 1990).

There are numerous anecdotes of spiders being found within or near the nests of ants (Elgar 1993; Cushing 1997 for review). These records suggest that there are two kinds of ant-associating spiders, myrmecomorphs and myrmecophiles, which probably evolved through different selection pressures. Myrmecomorphic spiders visually resemble ants, but generally do not prey on their models (Elgar 1993), although there are some exceptions (Cooper *et al.* 1990; Oliveira and Sazima 1984). The spiders' visual resemblance may reduce the risk of predation by visually hunting predators such as birds and wasps, which avoid ants but prey on spiders (Elgar 1993; Cushing 1997). In contrast, myrmecophilic spiders typically do not share much visual resemblance to ants, but may nonetheless be specialist predators on their associated species of ant (Elgar 1993; Cushing 1997).

The nature of spider–ant associations are poorly understood, and few studies have examined the ecological distributions of myrmecophilic arachnids and their host species (e.g. Shepard and Gibson 1972; Edmunds 1978; Porter 1985; Cole *et al.* 1994; Cushing 1995; Allan *et al.* 1996). Such studies are especially important for revealing details of the nature of the relationship between the ant and the arachnid associate. For example, Allan *et al.* (1996) found that the abundance of a specialist ant predator *Habronestes bradleyi* (Zodariidae) was more closely associated with the ritualised territorial behaviour of its ant prey *Iridomyrmex purpureus*, than the number of foraging ants, or the distance to the nearest nest. These data suggested that the alarm pheromone released by ants when engaged in territorial behaviour was used as a foraging cue by the spider, and this was confirmed experimentally (Allan *et al.* 1996).

In Australia, the green tree ant, or weaver ant, *Oecophylla smaragdina*, is found throughout the tropical coastal areas (Lokkers 1986). *O. smaragdina* constructs arboreal nests by weaving leaves together using silk that is produced by its larvae (Hemmingsen 1973; Wojtusiak and Godzinska 1993). Although *O. smaragdina* workers are largely arboreal (Hölldobler 1983), they also venture onto the ground to forage or to travel between trees when canopies do not interconnect (Jackson 1988). A mature colony can contain between 100 000 and 500 000 workers (Hölldobler and Wilson 1978), and may span as many as 12 trees and contain up to 150 nests (Way 1954). *Oecophylla* colonies are monogynous, with a single queen living for around eight years (Hölldobler 1983). *Oecophylla* have a minor and a major caste. Minor workers usually remain within the brood chambers where they tend larvae, whereas major workers defend the colony territory, assist with the care of the queen, and forage (Hölldobler and Wilson 1990; Lokkers 1990). Major workers are more numerous than minor workers, a feature unique to this genus (Hölldobler and Wilson 1990).

Major workers of *Oecophylla* aggressively defend their colony from intrusion by other species or by conspecifics from neighbouring colonies (Hölldobler 1983; Dejean 1990). They attack most arthropods they encounter, and consequently reduce the numbers of insects on the trees they inhabit (Lokkers 1990). As a consequence they have been used as biological control agents to reduce the damage caused by pest insects in coconut, tea, mango, cocoa and citrus trees (Vanderplank 1960; Room 1973). Despite the aggressive nature of *Oecophylla*, there are records of many Homoptera and Lepidoptera that form apparently mutualistic associations with these ants (Way 1954; Vanderplank 1960; Lokkers 1990).

Several spiders associate with ants from the genus *Oecophylla*, including the thomisids *Amyciaea albomaculata*, *A. lineatipes*, and *A. forticeps*, an undescribed theridiid, and the salticids *Myrmarachne foenisex* and *M. plataleoides* (see Elgar 1993; Cushing 1997 for review). While these species have some visual resemblance to *Oecophylla*, the ant-associating salticid, *Cosmophasis bitaeniata*, does not. However, the nature of the relationship between *C. bitaeniata* and *O. smaragdina* has not been investigated.

Here, we examine the distribution of *C. bitaeniata* with respect to that of *O. smaragdina*, and investigate experimentally the nature of the relationship between *C. bitaeniata* and *O. smaragdina*. Finally, since salticids are diurnally active and have excellent eyesight (Jackson and Pollard 1996), we examine whether *C. bitaeniata* uses visual cues to avoid contact with its host.

## Materials and Methods

### *The distribution of spiders on trees inhabited by ants*

The number of *C. bitaeniata* and the number of nests of *O. smaragdina* per tree were examined at two sites in tropical Queensland, Australia: Digby's Organic Orchard in Cape Tribulation, and a mango plantation at Majors Creek, 50 km south of Townsville in the foothills of the Mt Elliot Range. Almost all of the trees included in the survey were mango, *Mangifera indica*. All of the branches and leaves of each tree were searched visually to a height of 2 m and the number of nests of *O. smaragdina* and the number of *C. bitaeniata* were recorded to the nearest centimetre.

The distribution of *C. bitaeniata* was further examined at a finer scale by recording the distance of the spider from the nest of the ants. In this sample, 100 *C. bitaeniata* were located haphazardly from various trees and shrubs located on the campus of James Cook University, Townsville, and the distance of each spider to the nearest nest of *O. smaragdina* was recorded.

### *Nest characteristics of ants*

We examined whether *C. bitaeniata* were more likely to be found in certain types of nests by recording various characteristics of the nests of *O. smaragdina* and the invertebrate fauna found in each nest. Nests

were randomly selected from each tree or shrub in the following way. A trunk height and angle from north was randomly selected. The branch of the tree or shrub that was closest to this angle and height was identified, and the nest that came closest to a randomly selected distance along this branch was then chosen. This nest was removed from the tree using secateurs and placed in a plastic bag. The bag containing the nest was transferred to a 4°C refrigerator, where it was left for 1 h. The cooled nest was dissected and the number of *C. bitaeniata*, homopterans, cockroaches, major and minor ant workers, ant larvae, and the number of dead and fresh leaves were recorded. Using these procedures, 47 randomly selected nests were dissected in March 1995.

#### *Prey of spiders*

Anecdotal field observations indicated that the prey captured by *C. bitaeniata* included dipterans, homopterans and the larvae of *O. smaragdina*. Cannibalism was also observed on one occasion. The prey preferences of *C. bitaeniata* were quantified experimentally. *C. bitaeniata* ( $n = 172$ ) were collected from the field and individually housed in upturned plastic cups with moistened cotton wool. After five days without food, individual *C. bitaeniata* were provided with a cockroach, a homopteran, a minor worker, a major worker or a larva of *O. smaragdina*. The single prey item was placed against the inside of the plastic cup and we recorded whether *C. bitaeniata* began to feed on the prey item within 30 min.

Minor workers of *O. smaragdina* carry their larvae between their mandibles, and *C. bitaeniata* sometimes removed the larva from the minor workers. The frequency of this behaviour was quantified in the following way. A nest of *O. smaragdina* was collected from the field and placed in a 4°C refrigerator. After 20 min, 30 minor workers and 30 larvae of *O. smaragdina* were removed from the nest. A larva of *O. smaragdina* was placed with each minor worker, which she picked up and carried in her mandibles. The minor worker and larva were then placed in a plastic cup with a single *C. bitaeniata*. In each 15-min trial ( $n = 30$ ), we recorded whether *C. bitaeniata* removed the larva from the mandibles of the minor worker.

#### *Effect of visual signals on the frequency of contact between ants and spiders*

Preliminary observations suggested that *C. bitaeniata* could avoid contact with major workers by relying on visual cues. We examined this possibility experimentally by recording whether the frequency of contact between *C. bitaeniata* and major workers increased in darkness. Majors of *O. smaragdina* were collected from the field by removing a nest of *O. smaragdina* from a tree, using secateurs, and placing it in a plastic bag. Spiders were collected in plastic vials from the same colony as majors of *O. smaragdina*. Workers and spiders from different nests of *O. smaragdina* were used for each trial. The nest of *O. smaragdina* and the spider were transferred to a 4°C refrigerator for 4 min, thereby immobilising the spiders and ants. Fifteen randomly selected major workers were removed from the cooled nest with forceps and placed in a glass container (15 cm × 15 cm × 5 cm) together with the spider. The ants and spider were then left to acclimatise for 5 min at room temperature.

The individual *C. bitaeniata* and 15 major *O. smaragdina* workers were observed under either normal light conditions or in darkness using infrared light. Each trial lasted for 10 min. Two infrared diode arrays (880 and 950 nm), an infrared detection camera (28 mm lens), a video recorder and a monitor were used to record the behaviour of the ants and spiders under infrared conditions. The glass container was washed repeatedly in 70% ethanol and water between each trial to avoid chemical contamination between trials. The video recordings were viewed later, and the number of times that an *O. smaragdina* major worker came into contact with a spider was recorded.

#### *Activity of majors when confined with spiders and non-nestmate ants*

The response of *O. smaragdina* major workers to nestmate and non-nestmate ants, *C. bitaeniata* and its congeners *C. micans* and *C. micarioides* was examined in darkness under infrared light. In each treatment, 15 major workers of *O. smaragdina* were confined with either a nestmate major worker, a non-nestmate major worker, an individual *C. bitaeniata*, an individual *C. micans* or an individual *C. micarioides*. The experimental procedure followed the previous experiment, except that every trial was observed in darkness using infrared light. Ants and spiders were collected from different nests for each trial. In each trial, we recorded the activity of the 15 resident ants, and assumed that any increase in the activity of *O. smaragdina* reflected an alarm response (see Blum 1969). The level of ant activity was assessed in the following way. A randomly selected point on the video monitor was delineated using a 2.5-cm<sup>2</sup> piece of black tape. The tape remained in the same location for all of the trials. The number of times one of the 15 workers crossed the black tape was recorded for each trial, and this value was used as an indication of the level of ant activity.

## Results

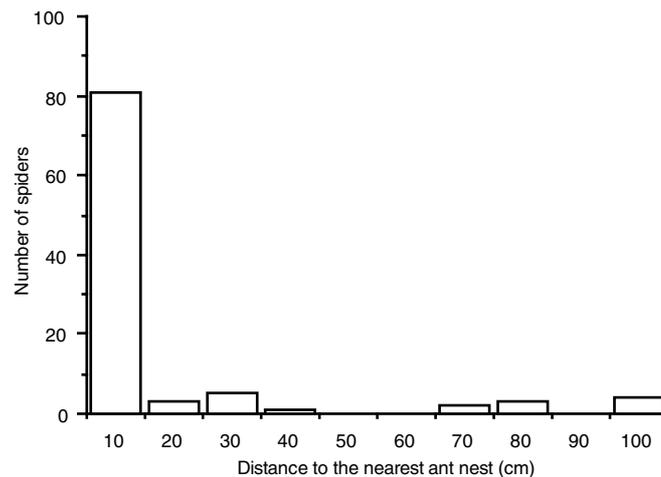
### *Ecological correlates of spider abundance*

The number of *C. bitaeniata* found on a tree was positively correlated with the number of nests of *O. smaragdina* on that tree ( $r = 0.63$ ,  $n = 46$ ,  $P < 0.001$ ). Additionally, *C. bitaeniata* was more likely to be found very close to the nests of *O. smaragdina*. Almost 80% of *C. bitaeniata* collected from trees and shrubs were found within 10 cm of an ant nest, with only 4% of spiders found further than 1 m from a nest of *O. smaragdina*. Assuming a random distribution of the numbers of *C. bitaeniata* along a 1-m length from an ant nest, the expected number of spiders within 10 cm of a nest would be 10, with 90 spiders found in the remaining distance. However, 79 individuals of *C. bitaeniata* were observed within 10 cm of the nest, compared with only 21 spiders found 10–90 cm from the nest. This observed distribution deviates significantly from the random distribution (Yates corrected  $\chi^2 = 93.6$ ,  $P < 0.001$ ; Fig. 1).

*C. bitaeniata* were present in or on 36% of the 130 nests of *O. smaragdina* that were surveyed in 47 trees. In total, 33 *C. bitaeniata* were collected, of which 26% were adult males; the remainder were either adult females or juveniles of unknown sex. Although up to 6 spiders were present in a single nest, there was never more than a single adult male found per nest.

Ant nests with *C. bitaeniata* contained significantly fewer major and minor workers than nests without *C. bitaeniata*; nests with spiders had roughly four times more ant larvae than nests without spiders (Table 1). The number of major workers of *O. smaragdina* was positively correlated with the size of the nest, indicated by the total number of leaves bound together ( $r = 0.426$ ,  $n = 47$ ,  $P = 0.003$ ). However, there was no evidence that the numbers of spiders was influenced by the size of the nest (Table 1). Older nests, estimated by the proportion of bound leaves in the nest that were dead, contained significantly more *C. bitaeniata* (Table 1) but the number of major workers of *O. smaragdina* was not correlated with nest age ( $r = -0.21$ ,  $n = 47$ ,  $P = 0.16$ ).

The larvae of *O. smaragdina* were readily consumed by *C. bitaeniata* in captivity, but spiders did not prey on minor or major workers of *O. smaragdina*. Spiders captured the



**Fig. 1.** Frequency distribution of the distance between *C. bitaeniata* and the nearest nest of *O. smaragdina*.

**Table 1.** Features of the nests of *O. smaragdina* and the distribution of *C. bitaeniata*  
*n* = 47 nests. Values are means  $\pm$  s.e

Characteristics	Nest of <i>O. smaragdina</i>		<i>t</i>	<i>P</i>
	With <i>C. bitaeniata</i>	Without <i>C. bitaeniata</i>		
Total no. of leaves bound within the nest	49.4 $\pm$ 11	43.4 $\pm$ 7.8	0.44	0.658
Percentage of dead leaves	61.8 $\pm$ 7.6	29.6 $\pm$ 6.7	3.16	0.003
No. of major ants	37.5 $\pm$ 15.2	148.7 $\pm$ 47.8	2.22	0.033
No. of minor ants	34.1 $\pm$ 15.7	125.2 $\pm$ 40.3	2.10	0.043
No. of ant larvae	25 $\pm$ 15.8	111.5 $\pm$ 41.3	1.96	0.058
No. of homopterans	8.6 $\pm$ 4.2	2.4 $\pm$ 2.4	1.29	0.204
No. of cockroaches	3 $\pm$ 0.8	0.7 $\pm$ 0.6	2.16	0.038

larvae held in the mandibles of the minor workers in 73% of the trials. Typically, the spider initially touched, with its front legs, the antennae and head of the minor worker holding the larva. The behaviour of the spider apparently encourages the worker to release her grasp of the larva, which is then picked up by the spider. *C. bitaeniata* fed less frequently on homopterans and cockroaches. It is not clear whether these insects form part of the prey of *C. bitaeniata* in the field. Homopterans and cockroaches were more abundant in nests with a higher proportion of dead leaves; there was no significant difference in the number of homopterans in nests with and without *C. bitaeniata* (see Table 1). This suggests that the number of spiders in nests of *O. smaragdina* is not influenced by the availability of other potential prey.

#### *Behavioural interactions between ants and spiders*

*C. bitaeniata* came into contact with their host ants infrequently during daylight, walking away whenever a worker came closer than 1 cm. However, the number of ant–spider contacts was greater in darkness. The mean number of contacts between spiders and ants per trial was  $3.70 \pm 1.39$  in normal light conditions, compared with  $26.90 \pm 5.29$  under infrared light conditions ( $t_{10} = 4.243$ ,  $P = 0.002$ ).

The non-nestmate ant treatment was excluded from the analysis because the 15 resident ants captured all non-nestmate workers a few minutes after the trial began. The level of ant activity was significantly different between the remaining four treatments ( $F_{3,23} = 6.53$ ,  $P = 0.002$ ). *Post hoc* tests revealed no significant change in the level of ant activity in the presence of *C. bitaeniata*, but increased activity in the presence of *C. micans* and *C. micarioides* (Table 2). However, the ants did not capture any of the spiders, which were able to jump to safety.

#### **Discussion**

Our data show that the salticid spider *C. bitaeniata* is commonly found close to the nests of the green tree ant, *O. smaragdina*, where it preys on the larvae within the nest. Most myrmecophiles physically contact individual workers while gaining entry to the nests of their ant host (Howard *et al.* 1990; Vander Meer and Wojcik 1982). However, *C. bitaeniata* avoids direct contact with the major workers, and the lower number of spiders in nests with more workers may arise because *C. bitaeniata* faces a greater risk of detection in nests with higher numbers of workers. In daylight, *C. bitaeniata* avoids contact with ants that come within 1 cm, but under infra-red light *C. bitaeniata* does not take evasive action, presumably

**Table 2.** The activity level of 15 major workers of *O. smaragdina* when confined with either a nestmate worker or an individual of one of three species of *Cosmophasis*

Statistical differences were detected using a Two-tailed Dunnett test, which was used to examine differences in the reactions of ants between nestmates and each of the three species of *Cosmophasis*

Treatment	Mean ant activity <sup>A</sup> ( $\pm$ s.e.)	Trials	Dunnett test ( <i>q</i> )	<i>P</i>
Nestmates of <i>O. smaragdina</i>	63.89 $\pm$ 10.23	9	–	–
<i>C. bitaeniata</i>	73.67 $\pm$ 10.23	9	9.78	0.85
<i>C. micans</i>	111.60 $\pm$ 13.72	9	47.71	0.03
<i>C. micarioides</i>	134.5 $\pm$ 15.35	9	70.61	0.01

<sup>A</sup>Measured as the frequency with which workers passed across a designated area.

because the spider cannot detect the ants. Once inside the nest, *C. bitaeniata* preys on unattended larvae, or removes larvae that are held in the mandibles of minor workers. This remarkable behaviour is apparently facilitated by tactile stimulation of the ant by the spider.

The predator–prey relationship between *C. bitaeniata* and *O. smaragdina* may be typical of other myrmecophilous arachnids that live in the nest of ants. Shepard and Gibson (1972) suggest that the relationship between *Continusa* sp., a salticid found in the nests of the ant *Tapinoma melanocephalum*, is mutualistic. Nests of *T. melanocephalum* occupied by *Continusa* sp. had more ant larvae than nests without spiders, suggesting that the presence of *Continusa* sp. enhances the reproductive output of the ant colony (Shepard and Gibson 1972). The nests of *O. smaragdina* with spiders also had larger numbers of larvae than those without spiders. The diet of *Continusa* sp. is not known, but if it includes the larvae of its host then it may, like *C. bitaeniata*, simply target nests with more ant larvae. Spiders may also associate with ants in order to gain access to myrmecophilous insects, such as coccids, which provide ant honeydew or other rewards (Edmunds 1978), but there is little evidence for this idea from the present study. A variety of insects associate with *O. smaragdina* (Hölldobler and Wilson 1990), but we never observed *C. bitaeniata* drinking the honeydew secretions from coccids, and only infrequently observed *C. bitaeniata* feeding on insects other than ant larvae.

Cursorial hunting spiders may comprise up to 5% of the diet of ants (e.g. Brüning 1991; Halaj *et al.* 1997), and Lokkers (1990) found that the number of spiders on trees with *O. smaragdina* was significantly less than that on trees without *O. smaragdina* (see also Peng *et al.* 1999). It is therefore surprising that *C. bitaeniata* is found adjacent to or within the nests of *O. smaragdina*. When individuals of *C. bitaeniata* touch the workers of *O. smaragdina*, they did not elicit any increase in the activity beyond that elicited by nest-mate ants. Thus, brief contact with a major worker apparently does not alarm the ant. In contrast, there was an increase in the activity level of workers of *O. smaragdina* that contact either of the congeners, *C. micans* and *C. micarioides*. Apparently, the ants recognise *C. micans* and *C. micarioides* as intruders and respond accordingly, which may explain why *C. micans* and *C. micarioides* are found infrequently on trees with ants while *C. bitaeniata* are relatively abundant. Nevertheless, these two species are able to escape capture by the ants through jumping away or off the substrate while still attached to a silk dragline. Several aphid hyperparasitoids and adult dipterans also avoid contact with ants by running and jumping away (Völkl and Mackauer 1993; Hübner and Völkl 1996). Similarly, the myrmecophilous cricket *Myrmecophilous* sp. avoids being attacked by ants by swiftly

running away (Akino 1996). Flight may not be a suitable defense mechanism for *C. bitaeniata*, which routinely lives in close association with *O. smaragdina*.

There are several explanations for larger numbers of *C. bitaeniata* being found within older nests. First, there may simply be a constant recruitment of unrelated individuals to the nest. Alternatively, the nests may be host to several generations of spiders if the offspring of resident spiders remain within the vicinity of the nest. We found eggsacs of *C. bitaeniata* either on or within the nests of *O. smaragdina*, but the dispersal patterns of spiderlings of *C. bitaeniata* are not known. Although salticids typically disperse by ballooning (Greenstone *et al.* 1987), spiderlings of *Aphantochilus rogersi*, which prey on ants, remain within the vicinity of their natal nest (Castanho and Oliveira 1997) and the same may be true of *C. bitaeniata*. Nevertheless, *C. bitaeniata* is characteristically solitary, and individuals placed in the same container are typically cannibalistic, suggesting that dispersal by spiderlings might be advantageous.

Nests of *O. smaragdina* are ephemeral, and thus *C. bitaeniata* of any age may have to locate new nests. It is not clear how *C. bitaeniata* locates new nests, but they may use a combination of visual and chemical cues. Salticid spiders have acute vision, which they use to great effect when capturing prey (Jackson and Pollard 1996), and *C. bitaeniata* may use visual cues to locate ant nests. Alternatively, the spiders may follow the surface chemical trails of *O. smaragdina*, as occurs in some myrmecophilic spiders (Cushing 1995; see also Quinet and Pasteels 1996) and other myrmecophilic insects (Dejean and Beugnon 1996). The zodariid spider *Habronestes bradleyi* uses alarm pheromones to locate its ant prey (Allan *et al.* 1996), and it is possible that *C. bitaeniata* also uses air-borne chemicals to locate ant nests.

Once a nest is found, *C. bitaeniata* is able to enter the nest, where it resides, despite the formidable chemical communication system of *O. smaragdina*, which is one of the most complex known for ants (Hölldobler and Wilson 1990). The workers use chemicals to lay down foraging trails, to provoke alarm and attack responses towards other species, to distinguish between nestmate and non-nestmate conspecifics, and to establish territories (Bradshaw *et al.* 1975; Hölldobler and Wilson 1978; Bradshaw 1981; Keegans *et al.* 1991). It is therefore remarkable that the workers of *O. smaragdina* do not attack or become alarmed when in the presence of *C. bitaeniata*. The key to the unusual predatory strategy of *C. bitaeniata* is chemical: the spider is able to live within the nest of *O. smaragdina* and feed on the ant larvae by masquerading as an ant (Allan 1998).

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### References

- Akino, T., Mochizuki, R., Morimoto, M., and Yamaoka, R. (1996). Chemical camouflage of myrmecophilous cricket *Myrmecophilus* sp. to be integrated with several ant species. *Japanese Journal of Applied Entomology and Zoology* **40**, 39–46.
- Allan, R. A. (1998). Cuticular hydrocarbon mimicry of the ant *Oecophylla smaragdina* by the salticid spider *Cosmophasis bitaeniata*. Ph.D. Thesis, University of Melbourne.
- Allan, R. A., Elgar, M. A., and Capon, R. J. (1996). Exploitation of an ant chemical signal by the zodariid spider *Habronestes bradleyi* Walckenaer. *Proceedings of the Royal Society of London, Series B* **263**, 69–73.

- Blum, M. S. (1969). Alarm pheromones. *Annual Review of Entomology* **14**, 57–80.
- Bradshaw, J. W. S. (1981). The physiological transmission of two components of a multiple chemical signal in the African weaver ant (*Oecophylla longinoda*). *Animal Behaviour* **29**, 581–585.
- Bradshaw, J. W. S., Baker, R., and Howse, P. E. (1975). Multicomponent alarm pheromones of the weaver ant. *Nature* **258**, 230–231.
- Brüning, A. (1991). The effect of a single colony of the red wood ant, *Formica polyctena* on the spider fauna (Araneae) of a beech forest floor. *Oecologia* **86**, 478–483.
- Castanho, L. M., and Oliveira, P. S. (1997). Biology and behaviour of the neotropical ant-mimicking spider *Aphantochilus rogersi* (Araneae: Aphantochilidae): nesting, maternal care and ontogeny of ant-hunting techniques. *Journal of Zoology* **242**, 643–650.
- Cole, D. C., Elgar, M. A., and Harvey, M. S. (1994). Associations between Australian pseudoscorpions and ants. *Psyche* **101**, 221–227.
- Cooper, D., Williamson, A., and Williamson, C. (1990). Deadly deception. *Geo* **12**, 87–95.
- Cushing, P. E. (1995). Description of the spider *Masoncus pogonophilus* (Araneae, Linyphiidae), a harvester ant myrmecophile. *Journal of Arachnology* **23**, 55–59.
- Cushing, P. E. (1997). Myrmecomorphy and myrmecophily in spiders: a review. *Florida Entomologist* **80**, 165–193.
- Dejean, A. (1990). Circadian rhythm of *Oecophylla longinoda* in relation to territoriality and predatory behaviour. *Physiological Entomology* **15**, 393–403.
- Dejean, A., and Beugnon, G. (1996). Host-ant trail following by myrmecophilous larvae of *Liphyrinae* (Lepidoptera, Lycaenidae). *Oecologia* **106**, 57–62.
- Edmunds, M. (1978). On the association between *Myrmarachne* spp. (Salticidae) and ants. *Bulletin of the British Arachnological Society* **4**, 149–160.
- Elgar, M. A. (1993). Inter-specific associations involving spiders: kleptoparasitism, mimicry and mutualism. *Memoirs of the Queensland Museum* **33**, 411–430.
- Greenstone, M. H., Morgan, C. E., and Hultsch, A.-L. (1987). Ballooning spiders in Missouri, USA, and New South Wales, Australia: family and mass distributions. *Journal of Arachnology* **15**, 163–170.
- Halaj, J., Ross, D. W., and Moldenke, A. R. (1997). Negative effects of ant foraging on spiders in Douglas-fir canopies. *Oecologia* **109**, 313–322.
- Hemmingsen, A. M. (1973). Nocturnal weaving on nest surface and division of labour in weaver ants (*Oecophylla smaragdina* Fabricius, 1775). *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening* **136**, 49–56.
- Hölldobler, B. (1983). Territorial behaviour in the green tree ant (*Oecophylla smaragdina*). *Biotropica* **15**, 241–250.
- Hölldobler, B., and Wilson, E. O. (1978). The multiple recruitment systems of the African weaver ant *Oecophylla longinoda* (Latreille) (Hymenoptera: Formicidae). *Behavioral Ecology and Sociobiology* **3**, 19–60.
- Hölldobler, B., and Wilson, E. O. (1990). 'The Ants.' (Belknap Press: Cambridge.)
- Howard, R. W., Akre, R. D., and Garnett, W. B. (1990). Chemical mimicry in an obligate predator of carpenter ants (Hymenoptera: Formicidae). *Annals of the Entomological Society of America* **83**, 607–616.
- Hübner, G., and Völkl, W. (1996). Behavioural strategies of aphid hyperparasitoids to escape aggression by honeydew-collecting ants. *Journal of Insect Behavior* **9**, 143–157.
- Jackson, R. R., and Pollard, S. D. (1996). Predatory behaviour of jumping spiders. *Annual Review of Entomology* **41**, 287–308.
- Jackson, R. V. (1988). Territorial defence and foraging in the ant *Oecophylla smaragdina virescens*. B.Sc.(Honours) Thesis, University of New England, Armidale.
- Lokkers, C. (1986) The distribution of the weaver ant, *Oecophylla smaragdina* (Fabricius) (Hymenoptera: Formicidae) in northern Australia. *Australian Journal of Zoology* **34**, 683–687.
- Lokkers, C. (1990) Colony dynamics of the green tree ant (*Oecophylla smaragdina*) in a seasonal tropical climate. Ph.D. Thesis, James Cook University, Townsville.
- McIver, J. D., and Stonedahl, G. (1993). Myrmecomorphy: morphological and behavioural mimicry of ants. *Annual Review of Entomology* **38**, 351–79.
- Oliveira, P. S., and Sazima, I. (1984). The adaptive bases of ant-mimicry in a neotropical aphantochilid spider (Araneae: Aphantochilidae). *Biological Journal of the Linnean Society, London* **22**, 145–155.
- Peng, R. K., Christian, K., and Gibb, K. (1999). The effect of colony isolation of the predacious ant *Oecophylla smaragdina* (F.) (Hymenoptera: Formicidae) on protection of cashew plantations from insect pests. *International Journal of Pest Management* **45**, 189–194.

- Porter, S. D. (1985). *Masoncus* spider: a miniature predator of Collembola in harvester ant colonies. *Psyche* **92**, 145–150.
- Quinet, Y., and Pasteels, J. M. (1996). Food and reproductive strategies of the myrmecophilous staphylinid beetle *Homoeusa acuminata* (Aleocharinae) on the foraging trails of its host ant *Lasius fuliginosus* (Hymenoptera: Formicidae). *Insectes Sociaux* **43**, 105–108.
- Room, P. M. (1973). Control by ants of pest situations in tropical tree crops: a strategy for research and development. *Papua New Guinea Agricultural Journal* **24**, 98–103.
- Shepard, M., and Gibson, F. (1972). Spider–ant symbiosis: *Cotinusa* spp. (Araneida: Salticidae) and *Tapinoma melanocephalum* (Hymenoptera: Formicidae). *Canadian Entomologist* **104**, 1951–1954.
- Vander Meer, R. J., and Wojcik, D. P. (1982). Chemical mimicry in the myrmecophilous beetle *Myrmecaphodius excavaticollis*. *Science* **218**, 806–808.
- Vanderplank, F. L. (1960). The bionomics and ecology of the red tree ant, *Oecophylla* sp., and its relationship to the coconut bug *Pseudothrips wayi* Brown (Coreidae). *Journal of Animal Ecology* **29**, 15–33.
- Volk, W., and Mackauer, M. (1993). Interactions between ants attending *Aphis fabae* ssp. *cirsiiacanthoidis* on thistles and foraging parasitoid wasps. *Journal of Insect Behavior* **6**, 301–312.
- Way, M. J. (1954). Studies of the life history and ecology of the ant *Oecophylla longinoda* Latreille. *Bulletin of Entomological Research* **45**, 93–112.

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