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SHORT COMMUNICATION

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Spectacular Batesian mimicry in ants

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Abstract The mechanism by which palatable species take advantage of their similarity in appearance to those that are unpalatable, in order to avoid predation, is called Batesian mimicry. Several arthropods are thought to be Batesian mimics of social insects; however, social insects that are Batesian mimics among themselves are rare. In Malaysia we found a possible Batesian mimic in an arboreal ant species, *Camponotus* sp., which was exclusively observed on foraging trails of the myrmicine ant *Crematogaster inflata*. The bright yellow and black colouring pattern, as well as the walking behaviour, were very similar in both species. We observed general interactions between the two species, and tested their palatability and the significance of the remarkably similar visual colour patterns for predator avoidance. Prey offered to *C. inflata* was also eaten by *Camponotus* workers in spite of their being attacked by *C. inflata*, indicating that *Camponotus* sp. is a commensal of *C. inflata*. An experiment with chicks as potential predators suggests that *Camponotus* sp. is palatable whereas *C. inflata* is unpalatable. After tasting *C. inflata*, the chicks no longer attacked *Camponotus* sp., indicating that *Camponotus* sp. is a Batesian mimic of *Crematogaster inflata*.

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Introduction

Batesian mimicry, where palatable species look similar to unpalatable ones to avoid predation, occurs widely in animals. Social insects are one of the most common "models" of Batesian mimics (Kistner 1979; Hölldobler and Wilson 1990; McIver and Stonedahl 1993; Cushing 1997), because social insects in general have strong defence mechanisms that are effective against predators. However, social insects that are Batesian mimics among themselves are rare. Possible Batesian mimicry has been suggested in a few ant species (Hölldobler and Wilson 1992; Gobin et al. 1998; Merrill and Elgar 2000), but experimental evidence using predators is lacking. In Malaysia, we found workers of the, as yet undescribed, formicine ant *Camponotus* sp. on foraging trails of the myrmicine ant *Crematogaster inflata*. *C. inflata* is a very rare ant species with a conspicuous yellow metathorax, which sharply contrasts with the otherwise black body. The metathorax is filled with a sticky fluid produced by the very large metapleural glands (Buschinger and Maschwitz 1984). The secretions contain toxic chemicals including 5-n-alkyl resorcinols (T. Akino et al., unpublished), which are suddenly discharged through the metapleural gland orifices when the ants are disturbed. The first gastral segment of the black *Camponotus* sp. is also bright yellow, giving it a high visual similarity to *C. inflata* (Fig. 1). When we found *C. inflata* colonies in Southeast Asia, we intensively looked for workers of *Camponotus* sp. on and near trails of *C. inflata* in order to study the basic interactions between both species in the field. Furthermore, by using predators, we tested the palatability of the two species and the significance of the remarkable black and yellow visual patterns for predator

Fig. 1 Two workers of the model (*Crematogaster inflata*, *left and middle*) and a mimic (*Camponotus* sp., *right*) sharing prey

avoidance. This is the first report of Batesian mimicry in ants, where observations have been supported by experimental evidence.

Materials and methods

Observations on interactions between *Camponotus* sp. and *Crematogaster inflata* and predator experiments were carried out in the Ulu Gombak field station in West Malaysia. To estimate the ratio of *C. inflata* workers to *Camponotus* sp. workers, we counted the number of workers found on six trails of one *C. inflata* colony for 10 min per trail. On each trail, dead insects were given as prey and the subsequent behaviour of the two ant species was observed.

For nestmate recruitment, *C. inflata* workers lay a trail pheromone from their hind leg tibia, as in other *Crematogaster* species (Leuthold 1968; Billen 1984). To check whether *Camponotus* workers can recognise the recruitment trail of *C. inflata*, we performed experiments with Y-shape bridges made from wooden sticks in the laboratory. We applied an acetone extract of crushed hind tibia on one branch, and acetone only as a control on the other branch. Workers were released at the base of the Y in order to check their choice at the bifurcation for either the trail extract or the control. Workers were released one by one, and new bridges were used for each worker.

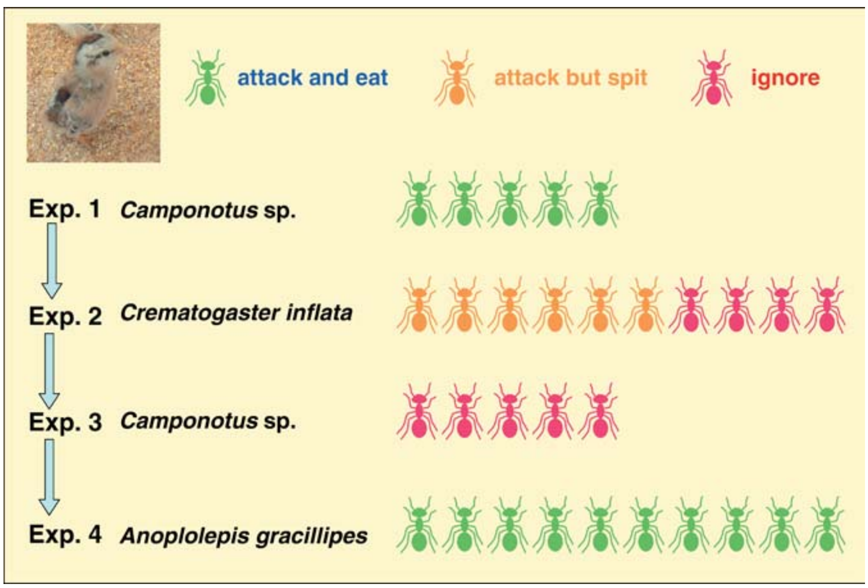
To test the palatability of the two ant species, we used chicks of Malaysian domestic chicken (n=14), which are known to consume several species of ants, including other species of *Crematogaster*. In the following experiments, carried out consecutively, we offered individual ants to individual chicks (Fig. 2). In a first experiment, we offered a total of five workers of *Camponotus*. Thereafter (second experiment), *C. inflata* workers were given to the chicks until they stop attacking. In a third experiment, *Camponotus* sp. workers were given again to chicks that had experienced the bad taste of *C. inflata* (n=12). To make sure the chicks did not avoid the *Camponotus* because of lack of hunger, in a final experiment we offered them workers of the ant species *Anoplolepis gracilipes* (Formicinae), which forms part of their normal diet.

Results

Workers of *Crematogaster inflata* follow trails in the vegetation. On the trails of all six studied *C. inflata* colonies from three different sites in Malaysia (Ulu Gombak and Endau Rompin in Peninsular Malaya, and Nabawan in Sabah), we found workers of the novel *Camponotus* species mentioned above (Fig. 1). This *Camponotus* species has never been observed independently of *C. inflata* colonies during our long experience in Ulu Gombak (more than ten field trips by F.I., representing a total of 6 months, and more than 2 years fieldwork by E.K.). During our fieldwork, we intensively looked for these ants in several trails in the forest of Ulu Gombak; however, we never found the novel *Camponotus* sp. except near *C. inflata* colonies.

Besides their visual similarity due to the bright yellow first gastral segment, workers of the mimic species raise their gasters while foraging, which is untypical for *Camponotus*. This behaviour, typical of *Crematogaster*, results in an even closer resemblance to *C. inflata*. *Crematogaster inflata* colonies nest in large cavities in tree trunks, while *Camponotus* sp. always nests in dead branches near

Fig. 2 Schematic representation of the experiment for testing the palatability of ants given to Malaysian domestic chickens



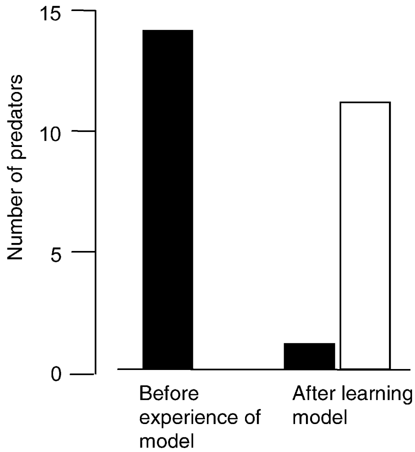


Fig. 3 Number of chicks attacking (*black*) and ignoring (*white*) the "mimic" *Camponotus* workers before and after learning the "model" *Crematogaster inflata*. All chicks (n=14) took *Camponotus* before experiencing the model (binomial test, P<0.001). All but two chicks learned to avoid the bad taste of the model after 2–7 trials. After learning of the model (n=12), all but one chick ignored the mimic (binomial test, P<0.01)

a *C. inflata* colony. The number of *Camponotus* workers counted on six different trails of one colony of *C. inflata* was small, with an approximate ratio of one *Camponotus* per 189 (±40 SE) *Crematogaster*. The number of *Camponotus* workers on trails of *Crematogaster* was equally low in the other five colonies. When we introduced dead insect prey near *C. inflata* trails of one colony (n=15), *C. inflata* workers quickly recruited nestmates. *Camponotus* workers also came to and fed on all but one of the offered bait insects, even though *C. inflata* workers always tried to repel them. A similar behavioural interaction was also frequently observed in the other colony in Ulu Gombak. This suggests that *Camponotus* sp. is a commensal of *C. inflata*, and that colour similarity does not help to avoid attacks by *C. inflata*.

In the laboratory experiment using Y-shape bridges, all but one of the workers of *C. inflata* followed the artificial trail of hind tibia extract (n=20, binomial test, P<0.0001), while *Camponotus* workers chose the two arms of the bridges randomly (n=44, binomial test, P>0.05), indicating that they do not reach the prey site by following *C. inflata* trails.

All chicks readily accepted workers of *Camponotus* sp., indicating that workers of *Camponotus* sp. are clearly palatable (Fig. 3, binomial test, P<0.001). In contrast, *C. inflata* workers appeared to be highly unpalatable: the chicks initially took the *C. inflata* workers but immediately spat them out. All but two chicks avoided *C. inflata* workers after 2–7 encounters with them. The chicks that had learned that the *C. inflata* ants tasted unpleasant (n=12) rarely tried to eat the *Camponotus* workers (Fig. 3, binomial test, P<0.01), suggesting that they remembered and learned from the bad experience with the similar-looking black and yellow *C. inflata*. All the chicks that had avoided *Camponotus* after their bad experience with *C. inflata* readily accepted several workers of *Anoplolepis*, indicating that these chicks were hungry, but nevertheless avoided *Camponotus* workers.

Discussion

In ants, possible Batesian mimicry has been reported in *Pheidole nastoides*, *Camponotus bendigensis* and *Polyrhachis rufipes*. Major workers of *Pheidole nastoides* look similar to soldiers of *Nasutitermes* termites, which have strong defensive chemicals (Hölldobler and Wilson 1992). Body size and colouring of *Camponotus bendigensis* are similar to *Myrmecia fulvipes*, which has a painful venomous sting, while the distribution of the two species largely overlaps (Merrill and Elgar 2000). *Polyrhachis rufipes* is often found on trails of *Gnamptogenys menadensis* in the Oriental tropics (Gobin et al. 1998), but is also occasionally collected outside the distribution range of *G. menadensis* (F. Ito, unpublished). *Polyrhachis rufipes* is a commensal of *G. menadensis* (Gobin et al. 1998). Workers of *P. rufipes* can follow the trails of *G. menadensis* and thus reach sugar sources even though *P. rufipes* workers are also attacked and repelled by *G. menadensis* workers from feeding sites (Johnson et al. 2003), as with the *Camponotus* sp. in our study. In these three cases, the supposed Batesian mimicry was based only on morphological similarity and sympatric occurrence without experimental evidence. Our data in the present paper provide the first experimental evidence of Batesian mimicry among ant species.

The most remarkable feature of *Camponotus* sp. in our study is that it always nests nearby and shares trails and food with its "model". Our experiment indicated that *Camponotus* workers do not follow recruitment trails of *C. inflata*. It must be confirmed in future whether *Camponotus* workers can actually recognise signals from *C. inflata* or whether discovery of the *Crematogaster* foraging sites just happens accidentally. Pfennig et al. (2001) have shown that the benefit of mimicry depends on the abundance of the model. If so, nesting in the direct vicinity to the model may be necessary for the evolution of Batesian mimicry in social insects. Nesting independently of the model may reduce the opportunity of learning by predators because social insect workers aggregate near their nests. This prerequisite may make Batesian mimicry very rare in social insects, in addition to the fact that social insects themselves develop defence mechanisms (Buschinger and Maschwitz 1984). In this respect, it would be interesting to know how *Camponotus* sp. finds *C. inflata* colonies in order to nest nearby. Alate queens of *Camponotus* sp. might be likely to choose their nesting site near *Crematogaster inflata*, but so far we have not had the chance to observe such behaviour in this very rare species.

Recently, Maruyama et al. (2003) described a new staphylinid beetle, *Drusilla inflatae*, collected near colonies of *C. inflata* in Ulu Gombak. As in *Camponotus* sp., the colour pattern of *D. inflatae* closely resembles that of *C. inflata*, and the beetle seems to be a Batesian mimic as well. The unpleasant taste of *Crematogaster inflata* has apparently resulted in the evolution of the mimicry syndrome.

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