The adaptive bases of ant-mimicry in a neotropical aphantochilid spider (Araneae: Aphantochilidae)

PAULO S. OLIVEIRA AND IVAN SAZIMA

Departamento de Zoologia, Universidade Estadual de Campinas, 13.100 Campinas, São Paulo, Brasil

The aphantochilid spider *Aphantochilus rogersi* accurately mimics black ants of tribe Cephalotini, and is commonly found in the neighbourhood of its models' nests. The mimic seems to be a specialized predator of this type of ant, rejecting any insect offered as prey other than cephalotines. In the field, *A. rogersi* was observed preying on the model species *Zacryptocerus pusillus*. In captivity, the spider preyed on the models *Z. pusillus* and *Z. depressus*, as well as on the yellow non-model *Z. clypeatus*. Recognition of correct prey by *A. rogersi* appears to be based primarily on visual and tactile stimuli. Capturing ant prey from behind was the most common attack tactic observed in *A. rogersi*, and is probably safer than frontal attacks, as in this case the spider can be bitten on the legs before the ant is immobilized. *Aphantochilus rogersi*, when feeding on the hard-bodied ant models, uses the ant corpses as a 'protective shield' against patrolling ants of the victim's colony and resembles an ant carrying a dead companion. Certain types of mimetic traits in *A. rogersi* (close similarity to ant models in integument texture and pilosity of body and legs), together with 'shielding behaviour', are thought to function as ant-deceivers, facilitating the obligatory intimate contact the mimic must make with cephalotines in order to capture a prey among other ants. The close similarity in the arrangement of dorsal spines, body shape, integument brightness and locomotion, together with antennal illusion, is regarded as a strategy of *A. rogersi* for deceiving visually-hunting predators that avoid its sharp spined ant models. It is proposed that ant-mimicry in *A. rogersi* has both an aggressive and a Batesian adaptive component, and evolved as a result of combined selective pressures exerted both by Cephalotini ant models (through defensive behaviour towards the mimics which attack them) and predators that avoid cephalotines (through predatory behaviour toward imperfect mimics). This suggestion is schematized and discussed in terms of two tripartite mimicry systems.

KEY WORDS: — Ant-mimicry – aphantochilid spider – cephalotine ants – natural selection – aggressive/batesian mimicry.

CONTENTS

INTRODUCTION

Ants serve as models for a great number of mimetic spiders belonging to distinct families. Among these, the Salticidae and Clubionidae contain by far the majority of ant-mimicking species, with both groups presenting an array of diverse morphological and behavioural ways of achieving an ant-like appearance (Peckham & Peckham, 1892; Reiskind, 1972, 1976, 1977; Edmunds, 1978; Oliveira, 1984). Several other spider families also have myrmecomorphic members (Reiskind & Levi, 1967), but it seems that mimetic specialization has reached an extreme within the Aphantochilidae. This family has four genera which mimic myrmicine ants of the tribe Cephalotini (Simon, 1895; Pocock, 1909; Levi, 1982). Two genera*, *Aphantochilus* Cambridge and *Bucranium* Cambridge, are known to prey upon their models (Piza, 1937; Bristowe, 1941). In this paper we present field and laboratory data suggesting that ant-mimicry in *Aphantochilus rogersi* has an aggressive component, so as to allow the mimetic spider to approach and capture cephalotine ants with a low risk of attack by the models. We also discuss other aspects of the resemblance of *A. rogersi* to its ant models, which seemingly cannot be attributed to this aggressive component alone.

MATERIALS AND METHODS

Field work was undertaken in different areas of Brazil between 1980 and 1983. Collections in Amazonian forest were made at the Estação Experimental de Silvicultura Tropical of Instituto Nacional de Pesquisas da Amazonia (INPA), Km 45 of the Manaus–Rio Branco highway (02°37'S, 60°02'W), State of Amazonas. In south-eastern Brazil individuals of *A. rogersi*, as well as cephalotine ants, were caught in the Reserva Biológica of the Instituto de Botânica de São Paulo, Mogi-Guaçu (22°18'S, 47°13'W), and in the Fazenda Dona Amélia Santo Antonio de Posse (22°35'S, 46°55'W), both in the State of São Paulo. Individuals of *A. rogersi* and ant models were also caught in central-western Brazil at the Fazenda São Sebastião, Santo Antonio do Leverger (15°55'S, 56°05'W) and the Reserva Ecológica Iquê (12°00'S, 59°24'W) of the Secretaria Especial do Meio Ambiente (SEMA), both in the State of Mato Grosso.

Individuals of *A. rogersi* and ants were sought out on plant and ground substrates. The behaviour of spider mimics and ant models as well as their responses to one another were observed in the field and under laboratory conditions. Each spider was maintained in a glass jar containing a piece of moist cotton and either short twigs or a small potted plant. Laboratory experiments were carried out intermittently with observation sessions lasting from 15 to 240 min. Potential prey, such as homopteran nymphs (Membracidae), fruit flies (Drosophilidae) and several ant species (models and non-models), were offered to *A. rogersi* in captivity.

*Piza (1937) described *Cryptoceroides cryptocerophagum* as a new genus and species of Aphantochilidae, which was later regarded by Mello-Leitão (1946) as a synonym of *Aphantochilus rogersi* Cambridge.

RESULTS

The morphological and behavioural adaptations of *A. rogersi* that account for its resemblance to black cephalotine ants are summarized in Table 1 (see also Figs 1–5 and Pocock, 1909; Bristowe, 1941).

Out of six individuals of *A. rogersi* found, five were observed on leaf surfaces and only one on the ground. On five occasions the spiders were observed in the vicinity of nests of their models. Predation upon ant models by *A. rogersi* was recorded twice in the field. At the subtropical savanna of Mogi-Guaçu, an individual of *A. rogersi* was observed on leaves carrying aloft a worker of the black cephalotine *Zacryptocerus pusillus* (Klug). On another occasion, at Santo Antonio de Posse, a spider was detected on a termite mound preying upon a worker among a group of *Z. pusillus* next to a hollow branch containing a colony of this ant species (Figs 1, 2). In this latter instance, the attack tactic employed by *A. rogersi* consisted of a rapid approach from behind, toward the back of the ant, followed by the seizure of the ant's petiole with the chelicerae and pedipalps (Fig. 1). After a subjugation period of approximately 5 min, the spider manipulated its prey with the first pair of legs and turned it round, so as to seize the dead ant by the neck (Fig. 2). While walking, the spider carried aloft its prey and kept from time to time the first pair of legs raised as 'antennae', and so appeared similar to an ant carrying a dead companion (Figs 2, 3).

In captivity, *A. rogersi* attacked and ate workers and soldiers of the black *Zacryptocerus pusillus* (a brownish worker was also preyed on) and *Z. depressus* (Klug), as well as those of the yellow non-model species *Z. clypeatus* (Fabricius)

Table 1. Morphological and behavioural mimetic analogy between *Aphantochilus rogersi* and its black cephalotine ant models

Spider mimic	Ant models
Shiny (sparse white hairs) and granular black integument	Shiny (sparse white hairs) and granular black integument
Cephalic region squared, posteriorly constricted	Squared head, separated from the thorax by a cervical region
Pair of lateral spines between cephalic and thoracic regions	Cephalic and/or pronotal lateral spines
Central cephalothorax with a long dorsal spine	Epinotal spines
Posterior cephalothorax double-constricted, pedicel lengthened	Epinotum, petiole and post-petiole
Oval abdomen, posteriorly banded with white hairs	Oval segmented gaster
Prominent chelicerae	Mandibles
Flattened legs, with sparse white hairs	Flattened legs, with sparse white hairs
Slow zig-zag locomotion	Slow zig-zag locomotion
First pair of legs raised	One pair of antennae
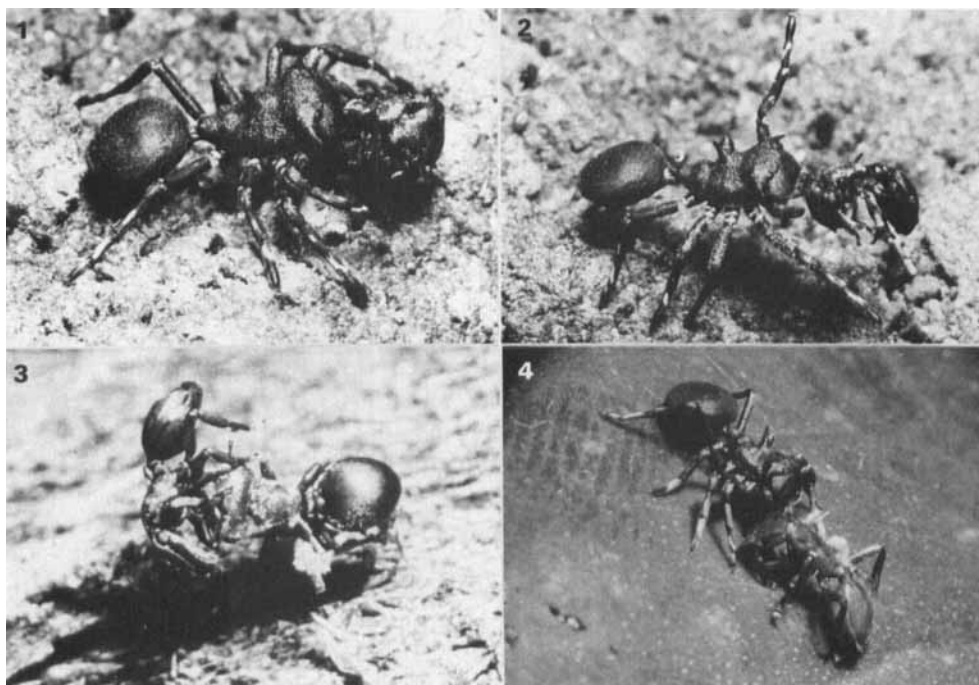
Figures 1–4. *Aphantochilus rogersi* (female) preying upon *Zacryptocerus* ants in the field and in captivity. fig. 1, *A. rogersi* capturing from the rear a worker of *Z. pusillus* on the ground close by a nest of this ant species. Fig. 2, The same spider carrying aloft the ant it had just killed; now *A. rogersi* 'seizes the ant by the cervical region. Fig. 3, A worker of *Z. pusillus* carrying a dead companion (compare with Fig. 2). Fig. 4, A captive individual of *A. rogersi* attacking frontally a worker of the yellow non-model species *Z. clypeatus*. Note the morphological resemblance between *A. rogersi* and *Z. pusillus*, particularly the shiny granular integument of both arthropods. Spider's actual size 6 mm.

(Fig. 4). This latter ant was more difficult for the spider to seize, as its integument is smoother than that of the model species. Out of 85 predation events of *A. rogersi* on *Zacryptocerus*, 63 involved attacks from the rear as observed in the field, whereas the other 22 consisted of frontal attacks and subsequent seizure of either the ant's head or neck (Fig. 4). In frontal attacks, *A. rogersi* kept its first pair of legs away from the ant's mandibles until the victim was immobilized. *Aphantochilus rogersi* may hold its prey from a few hours to three days before discarding the corpse. Careful examination of ant corpses discarded by the spider revealed that the ants were neither mutilated nor crushed, though they had their exoskeleton completely hollowed out.

While holding its prey, the spider may use the dead ant as a 'shield' against patrolling ants of the victim's colony. 'Shielding behaviour' was observed in captivity in a session with eight workers of *Z. pusillus*. Just after capturing one of the ants, the spider exposed the corpse toward any approaching ant; the latter ignored both after touching the dead body. If this shielding behaviour fails and mimic is treated by the victim's companions as an intruder, the spider can either flee from the disturbed ants to a safer place or jump off the leaf and hang by a silken line for some time before returning to the branch. Jumping behaviour was observed several times in captivity following sudden encounters between

A. rogersi and *Zacryptocerus*. On one occasion, the spider jumped off the leaf carrying a recently captured worker of *Z. pusillus*, as a result of being bitten on the legs by a patrolling ant.

The interaction between a large individual of *A. rogersi* caught with its first pair of legs missing, on a *Solanum* shrub (Solanaceae) in north Brazil, and eight workers of the large black cephalotine *Cephalotes atratus* (Linnaeus) was observed in captivity for 240 min. Most of the ants were tending *Tragopa* membracids at the apex of a potted *Solanum* branch. Eventually, one or two workers of *C. atratus* came down and walked on the lower leaves of the branch, where the spider was resting. On eleven occasions, when a wandering worker and *A. rogersi* met each other, the spider took refuge on the opposite surface of the leaf. On two other occasions, *A. rogersi* jumped off the leaf (suspending itself on a silken line for a few seconds) as a result of sudden encounters with *C. atratus* workers. Thirteen times the spider deliberately approached the ants on the apex of the branch, but returned to the lower leaves immediately after the ants became alarmed. During five of these approaches the mimic was able to touch the ants and once it seized a worker by the neck; however, as the victim's companions soon became alarmed, the spider released its prey and ran away from the disturbed ants.

In captivity, *A. rogersi* rejected any insects offered as prey other than cephalotine ants. Black *Camponotus* ants (Formicinae), *Drosophila* flies and membracid nymphs were not attacked, but the spider promptly attacked and ate *Zacryptocerus* ants offered after each session in which non-cephalotine prey items were rejected. *Aphantochilus rogersi* displayed strong avoidance reactions whenever it encountered workers of either *Camponotus crassus* Mayr or *C. blandus* (Fr. Smith); running away from the ant was the commonest escape behaviour. On one occasion a worker of *C. crassus* and another of *Z. pusillus* were offered simultaneously to an individual of *A. rogersi*. The spider apparently detected the moving *C. crassus* first, quickly approached it, touched the ant's gaster with the pedipalps and ran away afterwards. The slowly moving *Z. pusillus* worker was found soon afterwards and preyed on by the spider.

DISCUSSION

Predation on ant models

The close spatial association observed between *Aphantochilus rogersi* and its ant models provides strong evidence for mimetic specialization (see Wickler, 1968; Rettenmeyer, 1970; Edmunds, 1974, for examples with mimetic butterflies). The ant tribe Cephalotini contains more than 100 described species and all these seem to have similar arboreal and lignicolous nesting habits (Kempf, 1951, 1958; Wilson, 1971). Bristowe (1941) mentioned that *A. rogersi* is found in company with the large cephalotine *Cephalotes atratus* (= *Cryptocerus atratus* Linnaeus) and sometimes destroys its models. Piza (1937) caught twelve specimens of *A. rogersi* (= *Cryptoceroides cryptocerophagum* Piza) over a few days on a single plant where many workers of *Zacryptocerus pusillus* were also observed. Piza (1937) said further that each spider was carrying aloft an individual of *Z. pusillus*. The close proximity of most individuals of *A. rogersi* to caphalotine nests in nature strengthens the suggestion of a close biological relation between the spider mimic and its ant models.

The quick attacks on *Zacryptocerus* and the rejection of alternative non-cephalotine prey strongly suggest that *A. rogersi* is a specialized predator of cephalotines. Besides having preyed on all black *Zacryptocerus* ants (*Z. pusillus* and *Z. depressus*) offered in captivity, *A. rogersi* also ate one brownish worker of *Z. pusillus* and six individuals of the yellow *Z. clypeatus*, although the spider had more difficulty to seize this latter species. Recognition of correct ant prey appears to be based primarily on definite visual and tactile stimuli. When the captive *A. rogersi* quickly approached the moving worker of *Camponotus crassus*, the spider was plausibly being guided by visual cues emitting information of the type 'that animal looks and behaves like an ant'. However, running away from the ant soon after having touched it indicates the spider had probably received an information of the type 'this gaster is too pilose and/or soft to belong to a cephalotine'. Chemical stimuli may also play an important role for prey recognition in *A. rogersi*, since cephalotines are able to produce defensive secretions at the tip of the gaster (Coyle, 1966).

Capturing ant models from the rear was observed in the field, being also the most common attack tactic employed by *A. rogersi* during experiments in captivity where *Zacryptocerus* ants were offered as prey. This tactic is probably safer than attacking the ant's head, as in the latter case the spider runs an increased risk of being bitten on the legs before the ant is completely immobilized. It is possible that the absence of the first pair of legs in the large Amazonian specimen of *A. rogersi* was due to a predation failure. We suspect that, if this really happened, the spider lost its legs in a frontal attack on a large cephalotine prey, or the victim's companions detected and attacked the spider (both hypothetical situations could also have occurred simultaneously). Quite probably the failure of the Amazonian spider to capture workers of *C. atratus* in captivity was because it lacked its first pair of legs.

The method of subduing prey employed by *A. rogersi* appears to consist, as Turnbull (1973) mentions for almost all spider families, of a venom discharge delivered through the tip of the chelicerae which paralyses the victim. It seems that *A. rogersi* releases enzymes from the mouth into the body of the prey and sucks empty the digested body contents through the head-thorax joint of the ant. The fact that *A. rogersi* neither mutilates nor crushes its ant prey could be associated with the extremely hard integument typical of most cephalotines (Kempf, 1951, 1958). On the other hand, keeping its prey intact allows the spider either to use the ant corpses as a protective shield against patrolling ants, or to resemble an ant carrying a dead companion. We have observed a male of the thomisid *Strophius nigricans* Keyserling in the field carrying aloft a *Camponotus crassus* prey seized by its legs and held in much the same way as described for *Aphantochilus*. Although the thomisid bears no particular resemblance to its ant prey, except for size and colour, this behaviour rendered the spider an impressive ant-like disguise. A prey individual was held for hours and during encounters with ants in the laboratory the spider used the ant prey as a protective shield. Also, its hunting tactic was very similar to that described here for *A. rogersi*; the spider attacks its ant prey from behind and seizes it at the petiole until the ant is immobilized. These behavioural similarities between the two ant-preying spiders seem relevant in view of the supposed close taxonomic affinities between thomisids and aphantochilids (Simon, 1895; Reiskind & Levi, 1967; Levi, 1982).

Mimetic refinement, selective agents
and mimicry components

A close inspection of the adaptations for ant-mimicry in *Aphantochilus rogersi* (Table 1) reveals two major groups of mimetic traits. One group appears to consist of features that probably evolved in response to selective pressure exerted by the ant models, and another group seems to be formed by traits that evolved as a result of selective pressure exerted by visually hunting predators that avoid ants.

The close similarity of integument texture (granular) and pilosity of body and legs (sparse hairs) apparently facilitates the obligatory intimate contact *A. rogersi* must make with cephalotines in order to capture an ant among other ants. Mimetic traits like these could function as ant-deceivers and allow the spider to approach close to cephalotines without provoking immediate attacks from the ant models. Apparently, the ants may occasionally recognize the spider as an intruder by touching it with their antennae. Odour similarity between mimic and model could also play an important role for ant-deception, but this has not been investigated. The use of chemical substances associated with aggressive mimicry is already known for spiders (Eberhard, 1977). If ant-deceiving fails, the spider can still avoid being attacked by running away, jumping off (if on leaves) or shielding itself with an ant prey (which actually was shown to be an ant-deceiving behaviour). These escape responses strongly suggest that preying upon cephalotines is a dangerous habit and that the ant models are not at all defenceless. The experiments in captivity, during which the spiders were bitten on the legs by *Zacryptocerus* ants, support this view. Therefore, cephalotines may, by attacking less perfect mimics more frequently or readily, exert selective action for mimetic refinement in *A. rogersi*. This leads us to propose the existence of an aggressive component in this mimetic association. This hypothesis is supported by the fact that we have found no evidence from the arachnological literature about any spider, other than aphantochilids, preying upon cephalotine ants. Moreover, *A. rogersi* is closer in appearance and behaviour to cephalotine ants than to any other ant group.

Other types of mimetic resemblance between *A. rogersi* and its models, such as the close similarity in the arrangement of dorsal spines, body shape, integument brightness and locomotion, together with antennal illusion, provide strong circumstantial evidence that visually-hunting predators which avoid ants have exerted selective action for the evolution of ant-mimicry in *A. rogersi*. It is generally accepted that most hymenopterans are unpalatable to the majority of arthropod predators; and many innocuous animals, belonging to widely separated taxa, look similar to these noxious insects (see examples in Poulton, 1890, 1898; Mostler, 1935; Cott, 1940; Portmann, 1959; Brower & Brower, 1962, 1965; Wickler, 1968; Edmunds, 1974; Waldbauer, Sternburg & Maier, 1977; Opler, 1981; Oliveira, 1984; among others). Ants share with wasps and bees many characteristics which are sources of unpalatability; the most important are a potent sting (with associated venomous secretions, see Eisner, 1970), strong mandibles, toughness and distastefulness of the body. Bristowe (1941: 455) says that "Insectivores, reptiles and amphibia tend to leave ants alone, although there are exceptions to this, but they all relish spiders". Edmunds (1974: 115) states that ". . . few vertebrates regularly eat ants" and

Willis & Oniki (1978: 244) mention that "... few workers ants of any species are bird food." Among invertebrates, it is known that spider-hunting wasps show alarm at the approach of an ant (Peckham & Peckham, 1905). Bristowe (1941) believes that the vast majority of spiders avoid ants; the same author has also convincingly shown that several wandering spiders avoid attacking ant-mimicking spiders.

Although cephalotine ants neither sting nor have a fierce bite, the hard spined integument of most of the ants of this tribe may effectively protect them from any unspecialized enemy (Mann, 1916; Coyle, 1966). In fact, Wood (1975, 1977) has shown that a hard pronotum, combined with sharp dorsal pronotal horns capable of penetrating mouth tissue, can cause the rejection of some membracids by *Anolis* lizards. The same author also showed that the bizarre pronotal shape of these membracids, rather than their colour, can function as a visual signal for recognition and subsequent rejection by anoles (Wood, 1977). Analogously, the characteristic bizarre morphology of cephalotine ants could also provide warning cues to predators, who would avoid, through experience and stimulus generalization, similar appearing species. The apparently innocuous cephalotine-mimicking *A. rogersi* may gain some Batesian protection against predators that avoid its hard bodied ant models. Although we have not tested for Batesian mimicry in *A. rogersi*, there is much indirect evidence that it exists. Bristowe (1941: 449–450) writes the following about ant-mimicking spiders that prey on ants: "The fact that an ant-mimic will destroy its models is not in itself proof that the mimic is assisted by its appearance in doing so, and we must not forget that *most ants lack keen vision and depend to a much greater extent on touch and scent*. In fact we might with some justice argue that ant-like movements—*an ability to speak the ant-language, as it were—would be more important than a close structural resemblance*, and that there would be little survival value in anything more than similarity in colour and a rough approximation in size and shape" (our italics). On the same subject, Edmunds (1974) mentions that ants have poor eyesight and that aggressive ant-mimics, contrary to Batesian ones, are likely to bear only a superficial resemblance to their models in order to attack them without warning. If the assumptions of Bristowe and Edmunds are right, then why does *A. rogersi* look so similar to black cephalotine ants? Sexton (1970) showed that Batesian mimics which live in close sympatry with their models tend to be almost identical with them in appearance. According to Sexton, this would result from an improvement of the discriminatory abilities of predators resulting from frequently finding mimics and models together. In this situation natural selection for mimetic refinement should be strong. *Aphantochilus rogersi* has the closest possible spatial relationship with its model: it may carry a prey individual for hours or days, giving ample opportunity for discerning predators to distinguish and select against subtle differences in the spider. Thus it is likely that the answer to the question raised above relies on the fact that *A. rogersi* is commonly found in the proximity of its models' nests and frequently carries prey; the close structural resemblance between the spider and cephalotine ants would be a result of selective action exerted by visually hunting predators.

It seems therefore that *A. rogersi* benefits from its resemblance to cephalotines in two ways (see Hingston, 1928, on some Indian spiders; Brower *et al.*, 1960, on robberfly mimics): first, the spider would be able to approach closely and
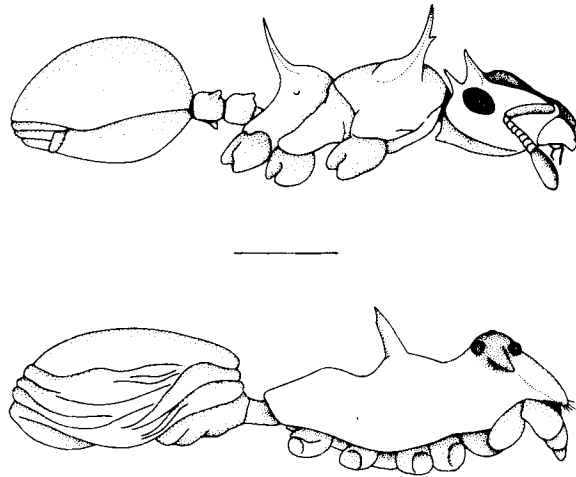
Figure 5. Lateral view of a worker of *Cephalotes atratus* (upper) and a large female of *Aphantochilus rogersi* (lower). Note the similarity between profiles of the ant model and its spider mimic. Scale bar = 2 mm.

capture cephalotines with partial impunity from attacks by the ant models (aggressive component); second, the spider would gain protection against predators that avoid cephalotines (Batesian component).

The mimicry of Cephalotini by Aphantochilus and the tripartite mimicry system

Vane-Wright (1976), developing a tripartite mimicry system originally presented by Wickler (1968), proposed a classification of mimetic resemblances in which mimicry is defined in terms of a system of three living organisms: model, mimic and operator (selective agent or signal-receiver). Vane-Wright's system stresses not only the biological role (negative or positive) of the operator relative to model and mimic, but also the interactive role (negative or positive) between the latter two (see Vane-Wright, 1976: 30–31).

The adjustment of the mimetic association between *Aphantochilus rogersi* and black cephalotines to Vane-Wright's tripartite mimicry system is schematized in Fig. 6. The scheme presents separately the two possible adaptive components (aggressive and Batesian) existing within this ant-mimicry system. In the aggressive component diagram, the operator and the model are connected by a dotted line, as they both belong to a given cephalotine model species (Fig. 6). Here the biological role of the operator to the model is positive, as they represent two ants of the same colony. On the other hand, the biological role of the operator to the mimic is negative, as the ant runs a high risk of being eaten by the mimic. The presence of the mimic is obviously a disadvantage to the model, and the interactive role between these two is negative. In the Batesian component diagram, each element of the tripartite system (model, mimic and operator) belongs to distinct species, and are graphically separated from each other by dotted lines (Fig. 6). The biological role of the operator (any ordinary predator of arthropods) to the model would be negative if we assume

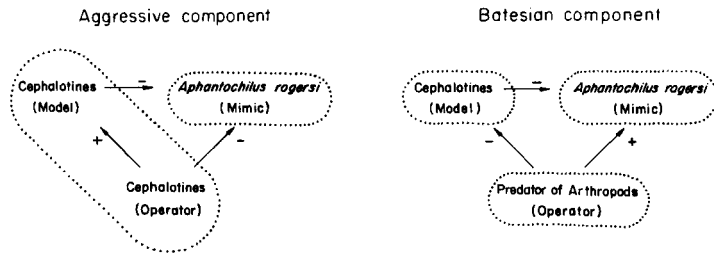Aggressive component   Batesian component

Figure 6. Scheme showing the two possible components (aggressive and Batesian) existing within the ant-mimicry of *Aphantochilus*, according to the tripartite mimicry system of Vane-Wright (1976). In the aggressive component diagram, operator and model both belong to a given cephalotine model species, and the biological role of the former to the latter is positive, for they represent two ants of the same colony. The biological role of the operator to the mimic is negative, as a given ant model runs a high risk of being eaten by the mimic. The presence of the mimic is evidently disadvantageous to the model, thus the interactive role between them is negative. In the Batesian component diagram, model, mimic and operator belong to different species. The biological role of the operator is negative to the unpalatable model, and positive to the innocuous mimic. The interactive role between mimic and model is negative, for the presence of a palatable mimic is clearly disadvantageous to a distasteful model.

that the hard horned integument of cephalotines causes rejection. However, the biological role of the operator to the mimic would be positive if we assume the latter as an innocuous potentially acceptable prey item. Thus, as the existence of the palatable mimic is disadvantageous to the distasteful model, the interactive role between them should be negative. These diagrams suggest how selective pressures from ant models and predators have provoked the evolution of mimicry in *A. rogersi*. Either one alone could be responsible for the development of this mimetic resemblance, but in our opinion only their combination can explain the remarkable similarity of *Aphantochilus rogersi* to its models both in general appearance (associated mainly with the Batesian component) and fine detail (due mostly to the aggressive component).

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