

On the mimetic association between nymphs of *Hyalymenus* spp. (Hemiptera: Alydidae) and ants

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Nymphs of *Hyalymenus*, unlike adults, have a highly differentiated ant-like morphology. Both *H. tarsatus* and *H. limbiventris* feed mainly on reproductive parts of composites and solanaceous plants, respectively. Mimetic nymphs were observed on plants, together with ants, both day and night; adult *Hyalymenus*, however, are predominantly nocturnal. Ant-resemblance in nymphs is achieved by several structural adaptations which, when coupled with the mimic's zig-zag locomotion and constantly agitated antennae, produces a striking visual deception. Experiments in captivity showed that mimetic nymphs, but not adult *Hyalymenus*, are somewhat protected against attacks from the praying mantid *Oxyopsis media* found on their host plant. Colour and size changes through different nymphal instars of *Hyalymenus* allow the immature bugs to resemble, during their development, differently sized and coloured ant models. Similar-looking ant species seem to act as Müllerian mimics toward insectivorous vertebrates and invertebrates that avoid ants. It is suggested that nymphs of *Hyalymenus* gain Batesian protection by resembling available ant models of different Müllerian complexes. Density-dependent selection is thought to be responsible for the observed differences in mimetic morph proportions between populations of mimics, as well as for the mimetic strategy itself employed by nymphs of *Hyalymenus*.

KEY WORDS:—Hemiptera – Alydidae – *Hyalymenus* – mimetic nymphs – Batesian ant-mimicry – ant Müllerian rings

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INTRODUCTION

Several families of Hemiptera include species that are strikingly ant-like at some phase of their life histories. Ant-mimicry (myrmecomorphy) has been

reported for the Alydidae (Nicholson, 1927; Mathew, 1935; Lima, 1940; Kormilev, 1953; Kumar, 1966; Schaefer, 1972; Elzinga, 1978; Sisson, 1980), Lygaeidae (Myers & Salt, 1926; Nicholson, 1927; Slater, 1982), Miridae (Nicholson, 1927; Lima, 1940; Edmunds, 1974; Jackson & Drummond, 1974), Pyrrhocoridae (Lima, 1940) and Reduviidae (Cott, 1940; Sharp, 1970).

The adaptive nature of ant-mimicry in hemipterans has never been tested in the field or under laboratory conditions. Nevertheless, most authors agree that ant-mimicking bugs would gain Batesian protection against visually hunting predators which avoid ants (Poulton, 1898; Myers & Salt, 1926; Nicholson, 1927; Mathew, 1935; Edmunds, 1974). Hymenoptera are generally well-protected against predators (Eisner, 1970; Blum, 1981). Furthermore, toads (Brower & Brower, 1962, 1965) and birds (Mostler, 1935) learn to avoid bees and wasps on sight after a few unpleasant experiences. Since ants share with bees and wasps many defensive traits (e.g. sting, secretion of acid substances, toughness of the body, distasteful flesh), it is very likely that the bugs are true Batesian mimics.

Genera like *Hyalymenus*, *Megalotomus* and *Riptortus*, in their nymphal stage, look and behave like ants; the adults, however, bear the typical shape of hemipterans (Mathew, 1935; Lima, 1940, and Figs 1–6). This study reports the morphological and behavioural traits responsible for ant-resemblance in nymphs of two Brazilian alydine bugs, *Hyalymenus limbatiiventris* Stål and *H. tarsatus* (Fabricius). Field observations on the interactions between *Hyalymenus* (nymphs and adults) and ants, together with laboratory experiments involving these bugs, ants and a praying mantid, provide circumstantial evidence of a selective value of ant-mimicry to alydine nymphs.

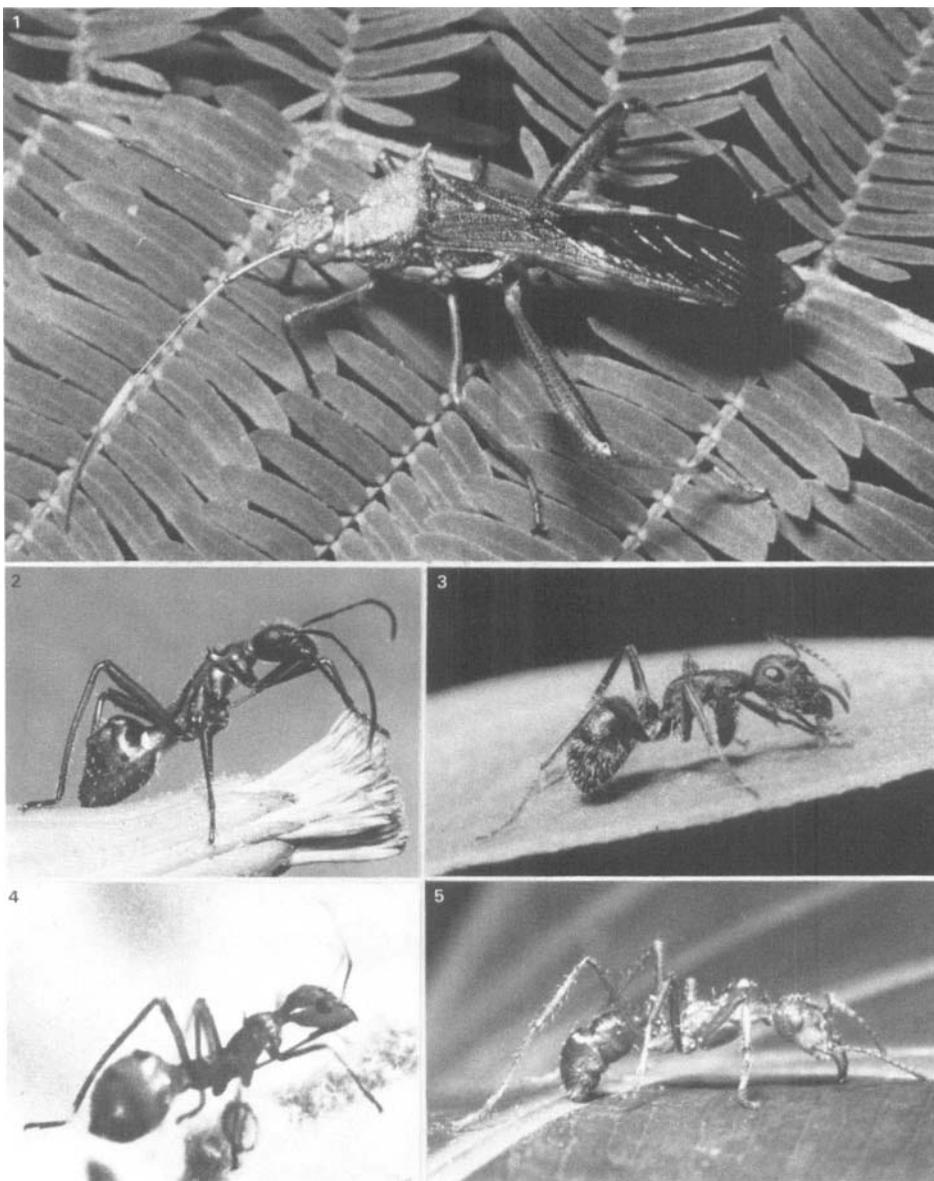
MATERIALS AND METHODS

Study sites

Field work was undertaken in different areas of Brazil between 1979 and 1982. In southeastern Brazil *Hyalymenus* bugs and ants were studied in the 'cerrado' (subtropical savanna) reserve of the Instituto de Botânica de São Paulo, in the municipality of Mogi-Guaçu (22°18'S, 47°13'W), state of São Paulo. Observations on ant-mimics were also made in a cerrado area of a private farm near the town of Perdizes (19°21'S, 47°17'W), state of Minas Gerais. Collections in tropical rainforest were carried out in the states of Acre and Amazonas. Field work in Acre was done in secondary growth vegetation of forest clearings near Cruzeiro do Sul (07°55'S, 72°57'W). Two study sites were used in Amazonas: the Estação Experimental de Silvicultura Tropical at km 45 of the Manaus-Boa Vista highway (02°37'S, 60°02'W) and the Agricultura Ecológica experimental area at km 42 of the same highway.

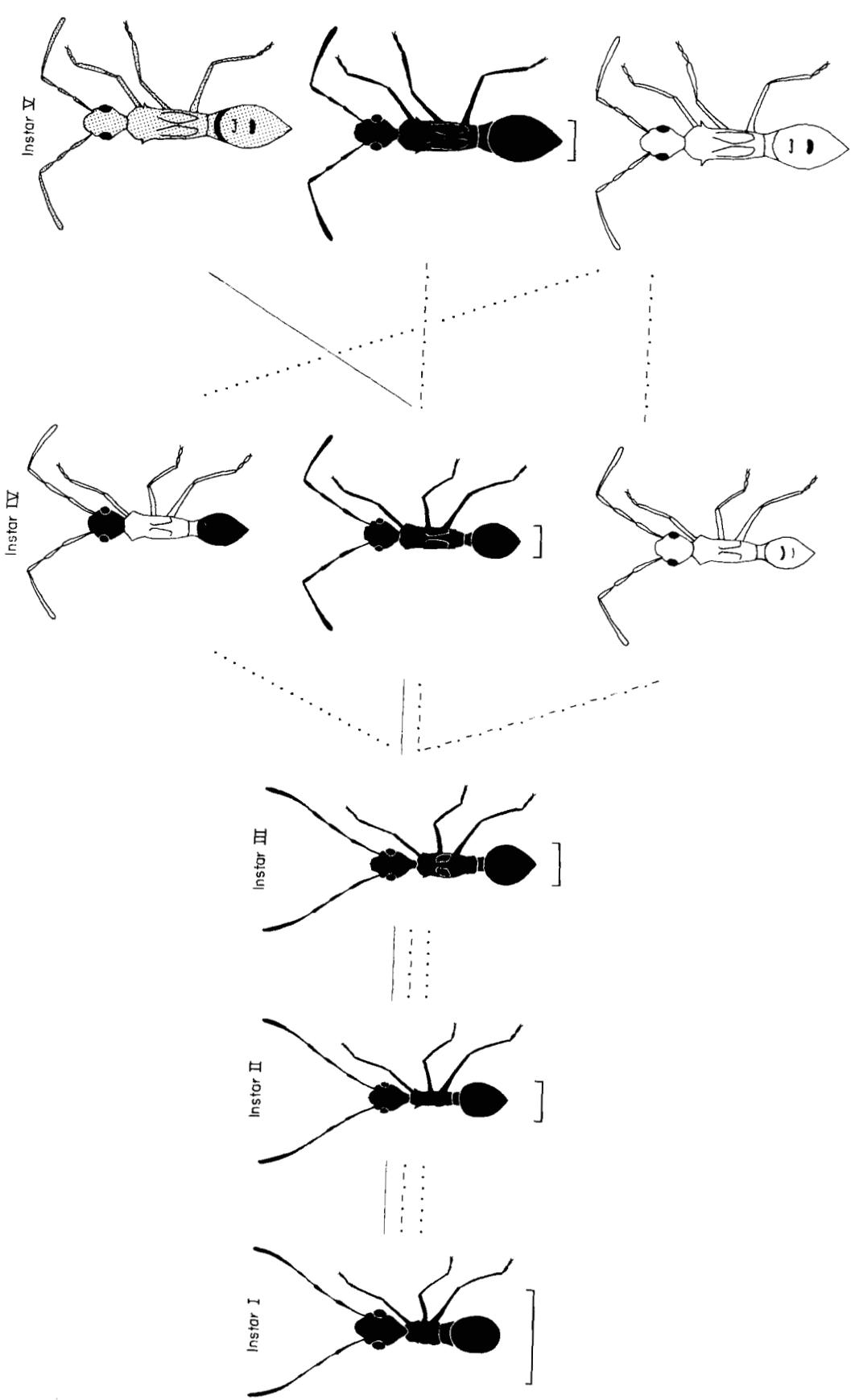
Surveys

The forest clearing at km 45 (hereafter Estação Experimental) was much smaller, and therefore closer to the neighbouring forest, than that at km 42 (hereafter Agricultura Ecológica), and its ant fauna included many yellow species typical of the dark forest interior. The proportion of differently coloured



Figures 1–5. Non-mimetic adult and ant-mimicking nymphs of *Hyalymenus*, and potential ant models for the nymphs. Fig. 1. Adult of *H. tarsatus*. Fig. 2. Black nymph of *H. limbativentris*. Fig. 3. Worker of a black *Camponotus* ant. Fig. 4. Yellow nymph of *H. limbativentris*. Fig. 5. Worker of the yellow ant *Ectatomma tuberculatum* (dead specimen). Note the typical hemipteran morphological pattern in the adult bug (actual size 1.5 cm), and the remarkably ant-like body profile of mimetic nymphs (actual size 1 cm).

(black or yellow) mimetic nymphs of *Hyalymenus limbativentris* and its relation to the ant fauna in both sites was investigated by surveying shrubs of *Solanum asperum* Vahl. (Solanaceae), which has especially attractive fruits for these bugs and several ant species. Thirty shrubs (1–3 m tall) were marked at each site. The presence of *H. limbativentris* (nymphs and adults), ants, and treehoppers



(Homoptera) was checked for all 60 shrubs. The number of bugs, the colour of mimetic nymphs and the number and colour of individuals of different ant species were recorded during a single 15 min census period for each shrub. After this initial census, 60 to 90 min were eventually spent at an occupied plant to make observations of the behavioural interactions between bugs and ants. Surveys of *Hyalymenus* and ants in the other study areas were carried out using qualitative methods.

The rearing of Hyalymenus and laboratory experiments

The morphological development of *Hyalymenus* nymphs was followed in captivity. The nymphs were reared in transparent plastic boxes containing fruits and/or flowers of the plants on which the insects were observed in the field. Eggs were obtained from captive adult bugs.

In captivity, experiments were carried out intermittently, with observation sessions lasting 15–60 min. Organisms were maintained in a 80 cm high vivarium covered with a cloth screen and containing a potted host plant to simulate natural conditions. One individual of *Oxyopsis media* (Stål) (Orthoptera: Mantidae) was used as potential predator of *Hyalymenus*. The interaction between *Hyalymenus* (nymphs and adults) and ants (models and non-models) was also investigated in the field through the observation of natural and provoked encounters.

RESULTS

Host plants and feeding behaviour of Hyalymenus

Table 1 summarizes the species and phenological states of plants on which nymphs and/or adults of *Hyalymenus tarsatus* and *H. limbiventris* were observed at different study areas. *Hyalymenus tarsatus* was observed feeding on flower and/or fruits of six plant species belonging to five families, being most frequently found on flower heads of composites. *Hyalymenus limbiventris* appears to feed exclusively on Solanaceae.

Nymphs and adults of *Hyalymenus* were observed in aggregations on reproductive parts of their host plants. The bugs insert the rostrum into the involucre bracts of composites (for *H. tarsatus*) or drupaceous fruits of *Solanum* (for *H. limbiventris*), and feed continuously on plant juices for several minutes. Occasionally the insect removes the rostrum completely from the bracts or fruits and usually cleans it with the first pair of legs. This behavioural sequence is repeated several times by the same bug on different parts of a reproductive branch. When fully satiated, the nymphs usually rest underneath leaves of the lower branches; adults may fly to other resting places.

Adult *Hyalymenus* are predominantly nocturnal; the nymphs, however, are active on host plants day and night. During the day, the greatest number of

Figure 6. Schematic outline showing colour and size changes through the nymphal instars of *Hyalymenus tarsatus* and *H. limbiventris* at different study areas in Brazil. Note that instars IV and V of *H. limbiventris* are dimorphic in Amazonas. ■, Black; □, yellow; ⊠, brown. --, *Hyalymenus tarsatus* in Cruzeiro do Sul and Mogi-Guaçu, ---, *H. limbiventris* in Amazonas;, *H. limbiventris* in Mogi-Guaçu. Scale bars = 2 mm.

Table 1. Plant species on which nymphs (n) and/or adults (a) of *Hyalymenus* spp. were observed feeding at different study areas in Brazil

<i>Hyalymenus</i> and plant species	Plant phenology	Study area	Bug stage
<i>Hyalymenus tarsatus</i>			
<i>Zeyhera digitalis</i> Mart. (Bignoniaceae)	FL	MO	n
<i>Baccharis dracunculifolia</i> DC. (Compositae)*	FL & FR	MO	n & a
<i>Erechtites hieracifolia</i> (L.) Rafin (Compositae)	FL & FR	AM-CS	n & a
<i>Casearia sylvestris</i> Sw. (Flacourtiaceae)	FL	MO	n
<i>Hortia brasiliana</i> Vand. (Rutaceae)	FR	PE	n & a
<i>Solanum granuloso-leprosum</i> Dunal. (Solanaceae)	FL & FR	MO	a
<i>Hyalymenus limbativentris</i>			
<i>Solanum granuloso-leprosum</i>	FL & FR	MO	n & a
<i>Solanum asperum</i> Vahl.†	VE, FL & FR	AM	n & a
<i>Solanum grandiflorum</i> Ruiz & Pavon.	FL & FR	AM	n & a

*Principal host plant in Mogi-Guaçu.

†Principal host plant in Amazonas.

MO, Mogi-Guaçu; AM, Amazonian sites; CS, Cruzeiro do Sul; PE, Perdizes. Plant phenology: flowering (FL); fruiting (FR); both (FL & FR); vegetative (VE).

adult *Hyalymenus* found on any given host plant was three, but as many as 15 were observed feeding or copulating on a single plant at night.

The mimics and their models

Nymphs of *Hyalymenus* have a highly differentiated ant-like morphology which is achieved by several structural adaptations (Figs 2–6, Table 2). The similarity is greatly enhanced by the nymph's ant-like behaviour, notably the rapid zig-zag locomotion, the constantly agitated antennae, and the up and down movement of the abdomen (similar to an alarmed ant). Adult *Hyalymenus* have a typical hemipteran shape, but their transparent hemelytra and brownish coloration produce a superficially wasp-like disguise (Fig. 1).

Colour and size changes through different nymphal instars of *Hyalymenus* allow the immature bugs to mimic, during their development, different castes of a given ant model species, as well as differently sized and coloured ant species (Fig 6, Table 3). Each size/colour category of nymphs is associated in Table 3 with a set of similar-looking ant species which are regarded as potential models in the different study areas. The exception is for instar IV of *H. limbativentris*,

Table 2. Morphological similarities between ants and mimetic nymphs of *Hyalymenus*

Ant characteristics	Adaptations for ant-mimicry in nymphs
Body with three well differentiated regions (head, thorax, gaster)	Cervical region thin, thorax and abdomen linked by a narrow 'waist'
Body, legs and antennae thin	Body, legs and antennae thin
Petiole between thorax and gaster	'Waist' lengthened
Mandibles large	Clypeus lengthened
Abdomen globose, anteriorly constricted	Abdomen globose, anteriorly constricted
Integument shiny and pilose	Integument shiny and pilose

Table 3. Coloration of different nymphal instars of *Hyalymenus* spp. and their respective potential ant models at different study sites in Brazil

Nymphal instars and study sites	Nymph colour	Potential ant models
<i>Hyalymenus tarsatus</i> Cruzeiro do Sul (Acre) and Mogi-Guaçu (São Paulo) First to fourth instar Fifth instar	Black Brown	Black <i>Camponotus</i> (e.g. <i>C. crassus</i> , <i>C. rufipes</i>), <i>Ecitonoma quadridens</i> Large dark ants
<i>Hyalymenus limbiventris</i> Agricultura Ecológica and Est. Experimental (Amazonas) First to third instar Fourth and fifth instars (Dimorphic)	Black Black or Yellow	Black <i>Camponotus</i> (e.g. <i>C. crassus</i> , <i>C. blandus</i>) Black <i>Camponotus</i> , <i>E. quadridens</i> Yellow <i>Camponotus</i> (<i>C. pitteri</i> , <i>C. latangulus</i>), <i>Ecitonoma tuberculatum</i> , <i>Pheidole biconstricta</i>
Mogi-Guaçu (São Paulo) First to third instar Fourth instar Fifth instar	Black Thorax yellow, head and abdomen black Yellow	Black <i>Camponotus</i> (e.g. <i>C. crassus</i> , <i>C. rufipes</i>) <i>Camponotus lespei</i> <i>E. tuberculatum</i> , <i>Camponotus pallens</i>

which is considered to be a species-specific mimic of *Camponotus lespesi* Forel in the cerrado area of Mogi-Guaçu (São Paulo). In this case, mimic and model have the same conspicuous colour pattern: thorax and legs yellow, head and abdomen black (with white hairs), antennae yellowish (see schematic outline of the mimic in Fig. 6). This similarity in body colour, together with the fact that *C. lespesi* is the only ant in Mogi-Guaçu with such a conspicuous appearance, seems to support the mimetic specificity proposed.

The proportions of black and yellow nymphs of *H. limbativentris* (instars IV and V are dimorphic in Amazonas, see Table 3, Fig. 6) differed significantly for the two Amazonian sites at which censuses were conducted ($\chi^2 = 4.25$, $df = 1$, $P < 0.05$). At the Agricultura Ecológica, only three of 44 nymphs observed were yellow, while at the Estação Experimental this morph represented 11 of 50 nymphs found. Differences between the colour patterns of the ant fauna, surveyed on shrubs of *S. asperum* at both Amazonian sites, were evaluated using the Mann-Whitney *U*-test for two independent samples (Sokal & Rohlf, 1981). The colour distribution within the two ant faunas were significantly different ($t_s = 6.339$, $P < 0.001$), indicating that there exists a much greater probability of finding a black ant species on a given shrub of *S. asperum* at Agricultura Ecológica than at Estação Experimental (see Fig. 7). Although the stinging yellow model *Ectatomma tuberculatum* (Olivier) (Fig. 5, Table 3) has not been registered on *S. asperum* shrubs at the latter site, it was commonly observed walking on leaves in the primary forest that surrounds the small clearing of the Estação Experimental.

The interaction between Hyalymenus and ants

Both under field and laboratory conditions, encounters between *Hyalymenus* (nymphs and adults) and ants were always provoked by the latter, followed almost invariably by a defensive reaction of the bugs. The defensive behaviour of mimetic nymphs during encounters with ants on the plants depends greatly on the type of ant.

Camponotus species (*C. blandus* (Fr. Smith), *C. crassus* Mayr, *C. lespesi*, *C. novogranadensis* Mayr and *C. trapezoideus* Mayr) never behaved aggressively toward *Hyalymenus* nymphs, irrespective of the bug's colour and size. Contact was usually restricted to a quick touch of the ant's antennae on either the nymph's antennae or legs. The commonest reaction of a nymph, when a *Camponotus* ant approached it, was to run away from the ant. On three occasions nymphs were observed jumping off leaves as a result of sudden encounters with workers of *C. crassus*, *C. lespesi* and *C. rufipes*. On the other hand, no nymph was ever observed abandoning a reproductive branch on which it was feeding as a consequence of encounters with *Camponotus* ants. In fact, on two different occasions a black nymph of *H. limbativentris* was found feeding on a fruiting branch of *S. asperum* among five workers of *C. crassus*. In each case the mimetic nymph fed continuously for 15 min without being disturbed by its models. On another occasion, a black nymph of *H. limbativentris* and a worker of *C. crassus* were observed simultaneously, during 15 min, on a single 1 cm diameter fruit of *S. asperum*; the nymph fed undisturbed on the fruit while the ant model tended immature membracids. During this period, two other workers of *C. crassus* that were wandering on the same branch also left the mimetic nymph undisturbed.

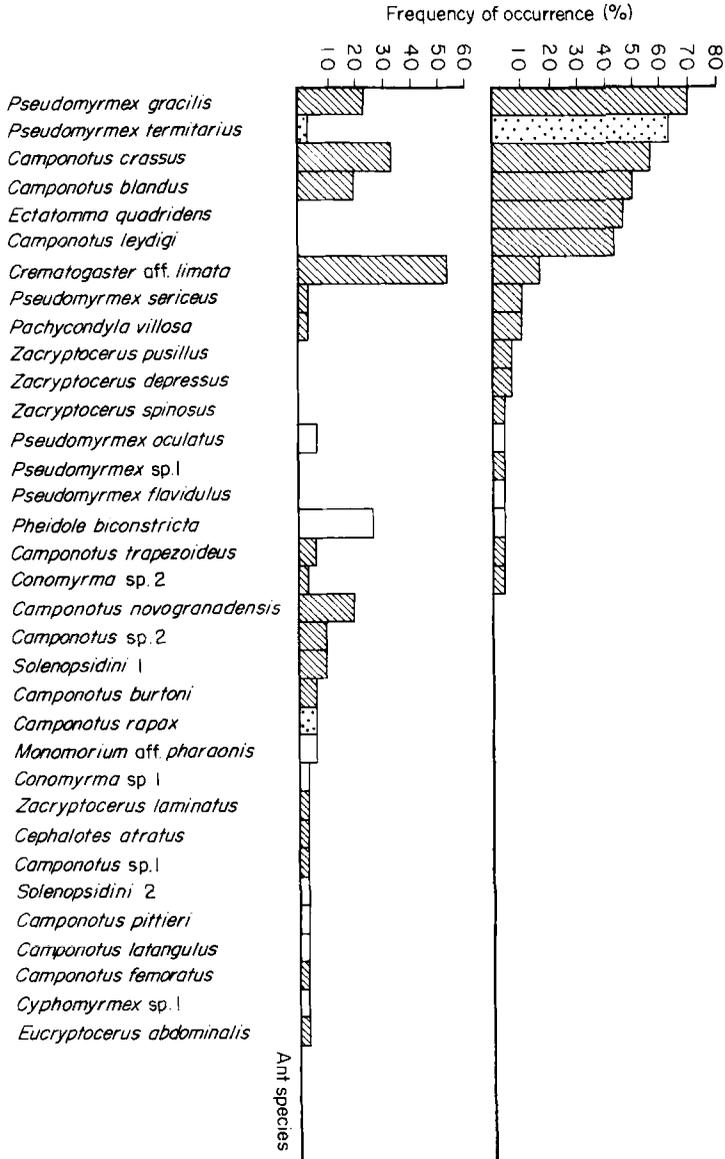


Figure 7. Frequency of occurrence of differently coloured ant species on shrubs of *Solanum asperum* in two Amazonian study sites, Agricultura Ecológica (right) and Estação Experimental (left), Brazil. Thirty shrubs were studied in each site. ▨, Black or dark; ▩, red and black mottled; □, yellow or light brown.

Finally, a black nymph of *H. limbiventris* was observed sucking a fruit of *S. asperum* among nine workers of the black model *C. blandus* which were foraging over the same branch.

Quite different behavioural interactions were observed between nymphs of *Hyalymenus* and *Crematogaster* ants, which have very populous colonies with highly efficient recruitment of the small workers to food sources (Wilson, 1971). Workers of *Crematogaster aff. limata* (Fr. Smith) were frequently observed in great

numbers on shrubs of *S. asperum*, and on one occasion more than a thousand workers were estimated on a single plant. The ants arranged themselves in many small aggregations over all the branches of the plant, but especially around the reproductive parts, and fed on sugar droplets from the plant itself or from honeydew-producing homopterans. Nymphs of *H. limbiventris* were attacked by *C. aff. limata* and *Crematogaster* sp. on fruits of *S. asperum* and *S. granuloso-leprosum*, respectively. In both cases attacks on black and yellow nymphs consisted of successive bites by one to three workers on the nymph's legs. Nymphs so attacked temporarily abandoned the fruits and descended to lower leaves. Such interactive sequences were observed on four consecutive occasions, during a 60 min observation session in the field, when one nymph of *H. limbiventris* and 13 workers of *C. aff. limata* were together on a branch of *S. asperum*. Both *C. aff. limata* and *Crematogaster* sp. were also observed expelling workers of *Camponotus crassus* and *C. trapezoides* from *Solanum* fruits.

The most conspicuous avoidance reactions displayed by nymphs of *Hyalymenus* during encounters with ants were those provoked by the approach of the large stinging ant *Ectatomma quadridens* (Fabricius). As soon as a given nymph detected a nearby worker of *E. quadridens*, it immediately ran away to another place or, more frequently, jumped off the branch. Such reactions took place even when the ant did not actively approach the nymph. Non-ponerine ants also show avoidance when they encounter *Ectatomma*.

Captive adults of *H. limbiventris* and *H. tarsatus* were attacked by workers of both *Camponotus crassus* and *C. blandus*. These attacks consisted of several bites on the legs of the adult bug, which then flew away from the potted plant. Under natural conditions, adult *Hyalymenus* were observed to avoid encounters with ants; a bug usually flies away when an ant approaches it.

Experiments under captivity with a praying mantid

One individual of the predatory mantid *Oxyopsis media* was used as potential predator to test whether nymphs of *Hyalymenus* gain any protection against invertebrate predators due to their resemblance to ants. This predator was chosen due to the fact that it was observed on a fruiting branch of *Solanum asperum* in Amazonas.

The first trial with *O. media* lasted 55 min and started 3 h after it was captured; during this time the mantid was deprived of food. One worker of the black *Camponotus femoratus* (Fabricius), *Ectatomma quadridens*, and one black nymph of *H. limbiventris* were separately offered, in this order, to *O. media*. The mantid clearly avoided both ant species: at any approach of the ants it walked away to the opposite side of the branch. On several occasions the ants touched one of the mantid's legs (either hind or middle), which was then rapidly raised, being lowered only after the ants had walked away. *Oxyopsis media* did not attempt to attack the mimetic nymph, and whenever the latter approached it the mantid walked to the opposite side of the branch.

The second trial with *O. media* lasted 50 min and was undertaken 3 days after the first trial (during this time the mantid was not fed). One worker of *Camponotus blandus* and one black nymph of *H. limbiventris* were separately offered to it, in this order. The ant bit the mantid's legs on three consecutive occasions; the predator then flew away. After being placed back on the fruits,

the mantid was again attacked by the ant, and flew away to a safer place in the vivarium. When the mimetic nymph was presented to it, *O. media* also avoided encounters with it, and on one occasion the predator raised its medium leg soon after the ant-mimic had approached it. Twenty hours later, still deprived of food, the mantid was given separately, in a 40 min session, one worker of *C. blandus*, one nymph and one adult of *H. limbiventris*, and one calliphorid fly, in this order. The predator's behaviour in relation to the ant and the nymph was quite similar. In both cases *O. media* kept still on the branch whenever the ant or the mimic approached it. On one occasion the nymph stayed for 10 s at only 1 cm from the predator's raptorial legs, and the mantid kept motionless after having detected the mimetic nymph. In contrast, the adult *Hyalymenus* was attacked twice by the mantid, but on both occasions the bug was able to escape. The calliphorid was promptly captured and eaten by the mantid.

DISCUSSION

Studies under natural conditions with bees and wasps have provided strong evidence that these stinging insects can form complexes ('rings') of similar-looking species, which act as Müllerian mimics in relation to their potential predators: unpalatable species within the complex all benefit from the reinforcement given by a unique aposematic pattern. Mimetic palatable dipterans associated with such complexes seem to gain Batesian protection against insectivores that have learned to avoid their noxious models (Waldbauer *et al.*, 1977; Plowright & Owen, 1980). It seems reasonable to suppose that similar-looking ant species could also form Müllerian rings (Reiskind & Levi, 1967; Oliveira, 1985). The noxious traits of most ants (cf. Eisner, 1970; Blum, 1981) have led many authors to believe that formicids are generally avoided by insectivores (Poulton, 1898; Cott, 1940; Bristowe, 1941; Wickler, 1968; Edmunds, 1974, 1976, among others). The quite repetitive morphology within the Formicidae (see Table 2), the typical zig-zag motion and the constantly agitated antennae of most ants could function as visual cues to predators, which would presumably avoid all of them.

Quite probably black *Camponotus* species form Müllerian rings in the study areas where they were observed foraging together. Besides biting fiercely, these formicines spray formic acid, a potent repellent for a variety of potential ant predators (Eisner, 1970). Species like *Camponotus crassus*, *C. blandus* and *C. rufipes* (among others), which have very populous colonies and co-occur in almost all regions of Brazil (Kempf, 1972), are so similar to each other that even an experienced myrmecologist cannot distinguish them at first sight. When black stinging ponerine ants, such as the common *Ectatomma quadridens*, are added to this supposed Müllerian ring the avoidance response of predators is perhaps reinforced. The same reasoning can be applied to a possible yellow Müllerian complex, evidenced at the Estação Experimental in Amazonas, involving *Pheidole biconstricta* Mayr, *Camponotus pittieri* Forel, *C. latangulus* Roger and *Ectatomma tuberculatum* (Table 3).

The ant-mimicking nymphs of *Hyalymenus* associated with ant Müllerian rings are almost certainly protected by Batesian mimicry against visually hunting predators that avoid ants. On the other hand, the existence of a Müllerian component in the resemblance between alydid nymphs and ants cannot be

discarded. The dorsal abdominal glands of these bugs are thought to be repugnatorial (Blum, 1981) and may have caused rejection by unspecialized predators. The experiments with *Oxyopsis media* suggest that the mimetic nymphs, in contrast to the non-mimetic adults, are at least partially protected against this type of predator. Besides not having attacked the ant-mimics, the mantid also behaved cautiously (walking away or raising one of its legs) at the approach of the nymphs. The learning capacities of arthropods are generally considered to be far less developed than those of vertebrates, but there is some evidence that certain spiders (Bristowe, 1941) and mantids (Rilling *et al.*, 1959; Gelperin, 1968) are able to discriminate visually and to avoid noxious prey. Selection for ant-mimicry in nymphs of *Hyalymenus* may have been exerted much more strongly by insectivorous vertebrates (particularly birds), since these animals have highly developed sensory organs and learn quickly to avoid distasteful prey. However, it seems more plausible to suppose that ant-mimicry in these nymphs evolved in response to combined selective pressures exerted both by vertebrates and invertebrates that avoid ants. The detailed structural and behavioural ant-like traits observed in the nymphs might be related to the fact that mimics and models are commonly found together on reproductive parts of plants. Such close spatial association provides ample opportunity for predators to distinguish mimics from models (cf. Sexton, 1960; Oliveira & Sazima, 1984); thus natural selection for mimetic refinement in nymphs would have been strong.

Several authors have followed Mathew (1935) in employing the term "transformational mimicry" for cases in which an animal mimics different models in different phases of its developmental stages (Reiskind, 1970; Jackson & Drummond, 1974). Such a situation was observed through the different nymphal instars of *Hyalymenus* and is probably advantageous to these ant-mimics for the following reasons (see Reiskind, 1970; Edmunds, 1978, on ant-mimicking spiders): (1) the mimic gains Batesian protection through all nymphal instars by resembling available ant models of similar size and colour; (2) the mimic can associate with various models, even in the same size/colour category, and its population as a whole seems less abundant relative to those of available models; (3) density-dependent predation on mimics is avoided. According to Benson (1977) a stable mimetic polymorphism can only evolve through density-dependent selection on a palatable mimic. This is probably the evolutionary path which ant-mimicking nymphs of *Hyalymenus* have followed. Thus the different proportions of black and yellow mimetic morphs of *H. limbiventris*, observed in the Amazonian sites, may reflect an avoidance of density-dependent predation, with different equilibrium points resulting from differences in colour distribution between the ant faunas of the two sites (Fig. 7).

Certain ant models may themselves have exerted some selective action for ant-mimicry in *Hyalymenus* nymphs. Particularly, the widespread *Camponotus* ants, which were never observed attacking their mimics but did attack adult *Hyalymenus*, appear to be deceived by the nymph's striking ant-like body profile (Figs 2-5). However, this needs more detailed investigation involving studies on ant communication. Field observations suggest that the presence of honeydew-producing homopterans can sometimes facilitate a peaceful coexistence between *Camponotus* and mimetic nymphs, since they draw the ants' attention away from other nearby animals. On the other hand, ants like the small *Crematogaster* seem

to defend effectively their food sources against any intruder, since a great number of workers are recruited to all attractive plant parts. Large stinging *Ectatomma* are so aggressive that a single worker is able to expel any insect, including other ants, from its food sources.

The predominantly nocturnal activity of adult *Hyalymenus* could be interpreted not only as a strategy to avoid predation from diurnal visually hunting predators, but also to avoid attacks from diurnal ants that commonly forage on their host plants.

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