

Myrmecophilous butterflies utilise ant–treehopper associations as visual cues for oviposition

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Abstract. 1. Selection of a safe oviposition site is important for herbivorous insects whose immature stages have limited mobility. Female herbivores rely on environmental cues for this choice, and presence of natural enemies or mutualistic partners may be important in this process.

2. Some butterflies have mutualistic interactions with ants (myrmecophily), in which caterpillars offer a nutritional liquid and gain protection against natural enemies. Participants in butterfly–ant mutualisms may utilise signals to initiate interactions, but the use of visual cues by ovipositing myrmecophilous butterflies remains uncertain.

3. Larvae of facultatively myrmecophilous *Parrhasius polibetes* (Lycaenidae) feed on *Schefflera vinosa*, and females prefer to oviposit near aggregations of the ant-tended treehopper *Guayaquila xiphias*, where caterpillars survive better due to increased ant attendance. Given the conspicuousness of ant–treehopper associations, it was investigated whether butterflies use them as visual cues for oviposition and, if so, which participants of the association are used as cues: ants, treehoppers, or both.

4. Experiments using dried insects on paired branches revealed that females visually recognise ants and ant–treehopper associations, using them for egg-laying decisions. However, presence of a treehopper aggregation alone had no effect on oviposition choices.

5. This is a first insight into the importance of visual discrimination for ovipositing myrmecophilous butterflies. The results show that facultative mutualisms can be important enough to promote a behavioural adaptation (visual detection of ants) reinforcing the interaction. Our research highlights the importance of the behavioural interface within complex multispecies systems.

Key words. Ant–butterfly interaction, cerrado savanna, host plant selection, mutualism, myrmecophily, oviposition behaviour.

Introduction

Choice of an oviposition site is important for lepidopterans and other herbivorous insects whose immature stages have limited mobility (Renwick & Chew, 1994). By choosing a high-quality site (i.e. less risky, more nutritious) to lay their eggs, females increase offspring survival and other aspects of immature performance, which ultimately may affect adult fitness (Thompson & Pellmyr, 1991). This choice is usually made by females through visual, olfactory, gustative and/or tactile cues from the host plant, such as leaf shape and colour,

secondary metabolites, and surface pilosity (Chew & Robbins, 1984; Renwick & Chew, 1994).

Finding a suitable and high-quality host plant is not the only problem faced by phytophagous insects; the risk of predation and parasitism accounts for a key source of mortality, and finding an enemy-free space is one of their most important challenges (Price *et al.*, 1980). In tropical regions, ants are important predators as they are extremely common on foliage (Jeanne, 1979; Floren *et al.*, 2002), where they find predictable resources such as extrafloral nectaries and exudate-producing hemipterans, and can complement their diet by hunting herbivorous insects (Davidson *et al.*, 2003; Rico-Gray & Oliveira, 2007). Indeed, butterflies may avoid ovipositing on plant locations occupied by ants more likely to kill larval offspring (Sendoya *et al.*, 2009). Although ants can be important agents

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of mortality for lepidopteran larvae, some butterflies in the families Lycaenidae and Riodinidae have evolved mutualistic interactions with ants (myrmecophily), in which caterpillars offer a nutritional liquid and gain protection against invertebrate enemies (DeVries, 1991; Pierce *et al.*, 2002). The level of interaction with ants varies strongly among these butterflies, ranging from facultative myrmecophiles that associate with many ant species but are not always found with tending ants, to obligate myrmecophilous species that associate with one or a few ant species and depend on them for survival. Although the proportion of species in each level of myrmecophily (facultative or obligate) varies across taxonomic groups and geographical regions, facultative interactions are the most common (Pierce *et al.*, 2002).

Myrmecophily requires both morphological and behavioural adaptations. The thick cuticle of lycaenid larvae and the presence of 'ant organs' specialised in the production of liquid rewards and in chemical and vibrational communication with ants are important morphological traits associated with myrmecophily (DeVries, 1990; Fiedler *et al.*, 1996). Among the behavioural traits of adults, ant-mediated egg-laying has been proposed for many species and experimentally shown for some, including *Ogyris amaryllis* Hewitson, *Jalmenus evora* Donovan, and *Maculinea teleius* (Bergsträsser) (Atsatt, 1981a; Pierce & Elgar, 1985; Van Dyck *et al.*, 2000; Wynhoff *et al.*, 2008), and may even result in oviposition on low-quality plants (Atsatt, 1981b; Rodrigues *et al.*, 2010). Ant-induced effects on oviposition have been studied more frequently in obligate myrmecophilous species and are thought to be weaker in the species that associate facultatively with ants (Wagner & Kurina, 1997). The use of chemical, tactile, and/or visual cues by butterflies in ant-mediated oviposition has been proposed for different systems, but without the support of experimental evidence (Pierce *et al.*, 2002).

Trager *et al.* (2013) consider that understanding how ants are detected by myrmecophilous butterflies as oviposition cues is a priority for future studies on the interaction between these organisms. Although visual detection of predacious ants has been shown to mediate ovipositing decisions in non-myrmecophilous butterflies that select less risky foliage for larval offspring (Sendoya *et al.*, 2009), the role of vision in oviposition decisions by myrmecophilous butterflies remains unclear. This can be further complicated if the butterfly–ant mutualism is affected by a third species, such as another ant-tended insect on the same host plant. For instance, oviposition decisions by the facultatively myrmecophilous lycaenid butterfly *Parrhasius polibetes* (Stoll) were recently shown to be mediated by the presence of ant–treehopper associations, near which ant-tended caterpillars survive better (Kaminski *et al.*, 2010). Due to the conspicuousness of ant-tended treehoppers (Fig. 1), this multispecies system provides an ideal situation to assess the role of different visual cues for ovipositing *P. polibetes*.

We used dried insects pinned to leaves to experimentally assess whether *P. polibetes* females are able to visually recognise ant–treehopper associations when searching for an oviposition site and, if so, which participants of the association are used as cues: ants, treehoppers, or both. Results revealed that female butterflies visually detect ants and ant–treehopper associations

on leaves and use them for egg-laying decisions. Given that caterpillars of this butterfly species use ants as bodyguards, this ability of females is crucial for increasing offspring survival. This shows that butterfly–ant facultative mutualisms can be relevant enough to promote a behavioural adaptation in ovipositing females (visual discrimination) reinforcing the interaction.

Organisms and methods

The study system

Parrhasius polibetes is a facultatively myrmecophilous lycaenid, whose larvae may be attended by several ant genera from the third instar on. It is a polyphagous species, recorded on flower buds of more than 80 plant species (Kaminski *et al.*, 2012) and showing different performance according to the host plant species (Rodrigues *et al.*, 2010; Rodrigues & Freitas, 2013). In the Brazilian cerrado savanna, one of its host plants is the shrub *Schefflera vinosa* (Cham. and Schldl.) (Araliaceae) (Fig. 1a,b) (Kaminski *et al.*, 2012). This plant species often harbours aggregations of the myrmecophilous honeydew-producing treehopper *Guayaquila xiphias* Fabr. (Membracidae; Fig. 1c), which attract more than 20 species of ants and show increased survival when tended by ants (Del-Claro & Oliveira, 1996, 1999, 2000). Ants tending *G. xiphias* eventually find and tend *P. polibetes* caterpillars as well (Oliveira & Del-Claro, 2005). Kaminski *et al.* (2010) showed that caterpillars growing on *S. vinosa* with ant–treehopper associations benefit from an enemy-free space, having greater survival rates in both the myrmecophilous and pre-myrmecophilous phases (see also Yoo *et al.*, 2013, for a similar case with ant-tended hemipterans). *Parrhasius polibetes* females utilise the ant–treehopper association as a cue for oviposition and preferentially lay their eggs on branches that host treehoppers and ants (Kaminski *et al.*, 2010). It is not known, however, if the cue is visual or olfactory, or which part of the association is more important.

Experiments

The experiments were performed at the Laboratório Nacional de Luz Síncrotron (22°48'S, 47°03'W), in Campinas, SP. The area is characterised as Cerrado *sensu stricto*, with shrubs and herbaceous plants. The experiments were conducted between February and June 2013, when the population density of *P. polibetes* is high in this area (Kaminski *et al.*, 2010).

Parrhasius polibetes females oviposit during the hottest hours of the day (10.00–16.00 hours). Females approach *S. vinosa* inflorescences with fast flights and, after alighting on a particular flower bud, spend from a few seconds to up to 3 min inspecting it with the legs, antennae and ovipositor before laying eggs or rejecting the bud. In the latter case, they fly to other flower buds in the same inflorescence or in nearby ones, usually within the same plant individual. After repeating this process for up to 10 min, females fly away very fast, ignoring other potential host plants nearby (more details in Kaminski *et al.*, 2010).

To evaluate the role of ants and treehoppers as visual cues for host plant selection by *P. polibetes*, we carried out a series of

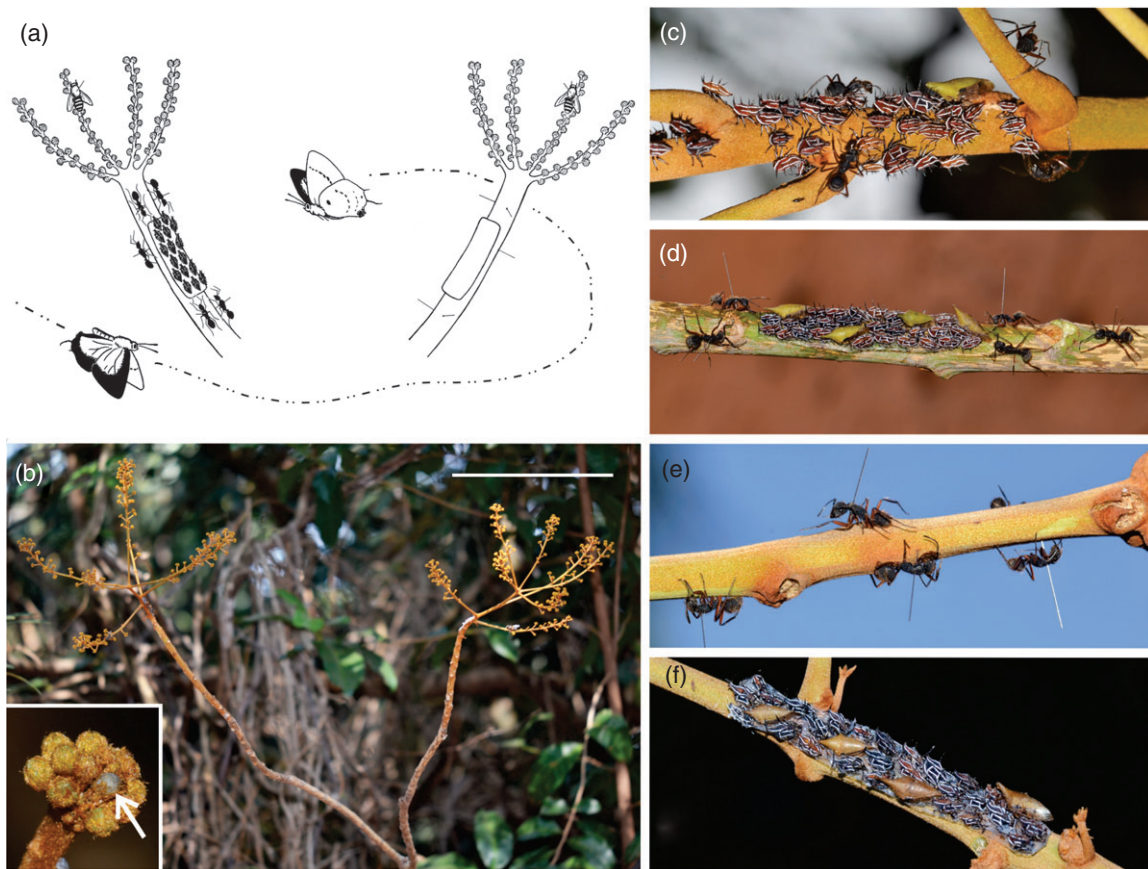


Fig. 1. Experimental setup for the oviposition trials with *Parrhasius polibetes* on branches of *Schefflera vinosa*. (a) Schematic representation of the experiments (elements not to scale). (b) General view of a pair of experimental branches in the field; scale bar, 25 cm. Inset photograph: egg of *P. polibetes* amongst floral buds. (c) Real association (live insects) of *Guayaquila xiphias* and *Camponotus rufipes* ants. (d) Simulated ant–treehopper association with dried insects. (e) Dried *C. rufipes* ants. (f) Simulated treehopper aggregation (dried insects). Butterfly ovipositions on experimental branches were checked after 24 h.

paired oviposition trials in the field using live insects or dried insects pinned to leaves (see also Freitas & Oliveira, 1996; Sendoya *et al.*, 2009). Approaching female butterflies were thus presented with a pair of branches (the control and the treatment), between which they could choose as an ovipositing site (Fig. 1a). Trials were performed using paired flowering branches of the same plant individual, to control for host plant quality. The branches in each pair were similar in size, and were from 0.5 to 1.5 m apart from one another (Fig. 1b). Non-experimental *Schefflera* branches were cut so that they would not interfere with butterfly choice, and special care was taken in pruning neighbouring foliage to ensure that both branches were easily seen by female butterflies.

We created four experimental treatments that we paired with control branches:

1. Real ant–treehopper association (i.e. live insects) as cues to butterflies (Fig. 1c). One treatment branch of *S. vinosa* had a real ant–treehopper association, whereas the control branch had no insects. Kaminski *et al.* (2010) showed that there is no difference in butterfly response between branches where the presence of treehoppers is natural or manipulated,

and thus we selected treatment and control branches with natural presence or absence of *G. xiphias* aggregations. We applied a sticky barrier of tanglefoot resin (Tanglefoot Co., Grand Rapids, Michigan) to control branches to prevent ant access. Treatment branches had resin applied on only one side so that ants could still reach the foliage.

2. Simulated ant–treehopper association (dried insects) as visual cues to butterflies (Fig. 1a,d). An aggregation of dried treehoppers (30 individuals; see Del-Claro & Oliveira, 1999) was glued on a transparent adhesive tape on the treatment branch, and five dried ants were pinned as if tending the treehoppers and walking nearby. Control branches received five pins, glue, and adhesive tape (Fig. 1a); branches did not harbour real treehopper aggregations prior to the experiment.
3. Only ants as visual cues (Fig. 1e): five dried ants were pinned at the base of the treatment branch, whereas control branches received only five pins. Branches did not harbour real treehopper aggregations prior to the experiment.
4. Only dried treehoppers as visual cues (Fig. 1f): an aggregation of dried treehoppers was glued on a transparent adhesive tape at the basis of the treatment branch. Control

branches received glue and adhesive tape. Branches did not harbour real treehopper aggregations prior to the experiment.

Experimental groups in series (2), (3) and (4) were established by a coin flip, and tanglefoot resin was applied to the base of both branches to prevent ant access. One dried honeybee was pinned on all experimental branches (Fig. 1a) to control for the presence of other insects that could visit *S. vinosa* shrubs and that might affect egg-laying butterflies (honeybees were collected at urban sites in Campinas). Experimental branches were established at 08.00 hours, and were carefully searched for *P. polibetes* eggs after 24 h (Fig. 1b); eggs were then manually removed.

Insects and materials used in the experiments

Observations of the ovipositing behaviour of *P. polibetes* were made at the Laboratório Nacional de Luz Síncrotron from January to August 2013, during the day (08.00–17.00 hours). Females were observed and followed until flying out of sight.

Treehoppers and ants were collected in three cerrado sites near Campinas, São Paulo State, southeast Brazil. The ant species used was *Camponotus rufipes*, because of its large size, which facilitates mounting and visualisation. Moreover, *C. rufipes* is one of the species most frequently found associated with *G. xiphias*, tending the treehoppers day and night (Del-Claro & Oliveira, 1999). Previous experiments on oviposition behaviour of *P. polibetes* were also performed using *C. rufipes* (Kaminski *et al.*, 2010).

All the insects were taken to the laboratory, frozen, and then dried in an oven for at least 1 day. Ants were washed in *n*-hexane for 5 min before mounting, to eliminate their cuticular hydrocarbons (see Silveira *et al.*, 2010) and control for possible effects on butterfly oviposition behaviour. This procedure was not necessary for treehoppers, as it is known that their cuticular hydrocarbons are similar to the host plant *S. vinosa* (Silveira *et al.*, 2010).

Ants were mounted with a thin pin (Bioquip no. 0.20; Rancho Dominguez, California), simulating the posture of live individuals (see Fig. 1d,e). Groups of treehoppers were glued with silicon glue (Cascola; Henkel Co., São Paulo, Brazil) on a piece of transparent adhesive tape (Adelbras; Adelbras Tech, Vinhedo, Brazil), resembling a natural aggregation (Fig. 1c). Simulated treehopper aggregations consisted of 30 individuals, four to five of them adults and the others last-instar nymphs, compatible with the range observed in the field (Del-Claro & Oliveira, 1999, 2000).

Statistics

A total of 40 plants were used in the 24 h oviposition trials to reach a sufficient number of valid branch pairs. Individual plants could be reused during the period of experiments. Because oviposition trials were performed during the period of highest butterfly abundance, egg-laying decisions were assumed to be independent (i.e. made by different females). Only branch pairs receiving at least one egg were considered for the analyses. Difference in the proportion of branches with and without eggs was evaluated through G-tests with Williams correction.

The difference in the number of eggs found in treatment versus control branches was evaluated through Wilcoxon paired test. The tests were performed using BIOSTAT 5.0 (Instituto Mamirauá, Tefé, Brazil).

Results

Branches with live ant–treehopper associations were chosen for oviposition by *P. polibetes* females significantly more often than those without associations (Fig. 2a), and received greater numbers of eggs (Fig. 2e). Branches hosting dried ant–treehopper associations were chosen for oviposition more often than control branches without dried ants and treehoppers (Fig. 2b), and also received increased numbers of eggs (Fig. 2f). Branches with pinned dried ants were chosen for oviposition more often than control branches with pins only (Fig. 2c), but the number of eggs did not differ between experimental branches (Fig. 2g). The presence of dried treehopper aggregations had no effect on *P. polibetes* females, either as a site for oviposition (Fig. 2d) or on the number of eggs laid (Fig. 2h).

Discussion

Our results showed that myrmecophilous *P. polibetes* are able to visually detect ants and ant–treehopper associations, and use them as cues in the oviposition process. In addition, we showed that the presence of ants alone is enough to elicit a response by egg-laying females. In antagonistic relationships, the ability of egg-laying butterflies to recognise and avoid ants through vision has already been demonstrated for *Eunica bechina*, whose caterpillars are frequently attacked by ants on the host plant (Sendoya *et al.*, 2009). Both butterfly species rely on the same cue – the image of ants – to choose an enemy-free space for oviposition, but react to it in opposite ways, depending on the effect from ants on caterpillars: predation in the case of *E. bechina* (Sendoya *et al.*, 2009) and protection in the case *P. polibetes* (Kaminski *et al.*, 2010). These contrasting responses demonstrate the importance of the female's oviposition behaviour for offspring survival in these two butterflies. The degree to which *P. polibetes* females are also able to visually distinguish among different ant species, as shown for the nonmyrmecophilous *E. bechina* (Sendoya *et al.*, 2009), awaits further investigation (but see Fraser *et al.*, 2002).

In the studied system, *G. xiphias* aggregations play a very important role in the generation of the enemy-free space enjoyed by immature *P. polibetes*, as the presence of treehoppers attracts ants to *S. vinosa* shrubs (Del-Claro & Oliveira, 1996, 2000). However, our results show that the presence of a treehopper aggregation alone does not affect oviposition decisions of *P. polibetes*. Considering that the ants are the organisms directly interacting with the caterpillars and protecting them from natural enemies, it is reasonable to expect that their presence on foliage should be more relevant than that of treehoppers for a female's oviposition decision. Indeed, 90% of the food plants (40 species) utilised by *P. polibetes* bear ant attractants such as extrafloral nectaries or honeydew-producing hemipterans (Kaminski *et al.*, 2012; Alves-Silva *et al.*, 2013), which make the image of ants a recurrent trait on foliage. Thus female butterflies

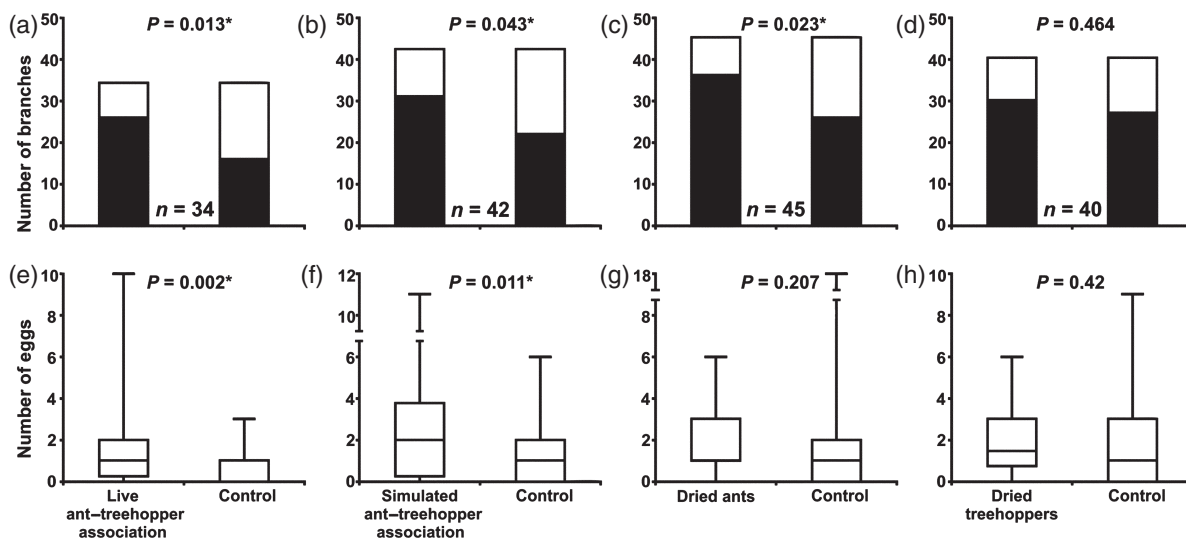


Fig. 2. Oviposition patterns for the butterfly *Parrhasius polibetes* in choice experiments (24 h), using paired branches of *Schefflera vinosa*. (a–d) Branch selection for oviposition by butterflies (black bars, branches with eggs; white bars, branches without eggs). (e–h) Number of eggs laid per branch (boxes show the lower and upper quartiles and whiskers show the total range). (a,e) One branch presented the association between the treehopper *Guayaquila xiphias* and tending ants, while the other did not present any insects. (b,f) One branch received a simulated ant–treehopper association with dried insects, while the control did not have insects. (c,g) One branch presented five dried ants, while the other did not present any insects. (d,h) One branch received a simulated treehopper aggregation with dried insects, while the control did not have insects. An asterisk denotes a significant difference between treatments.

capable of visually recognising ants would be more efficient in the choice of an enemy-free space for oviposition than those only able to recognise one or some of the ant attractants present in all potential host plants. On the other hand, when the presence of treehoppers and ants is combined, *P. polibetes* females lay increased numbers of eggs. Treehopper aggregations may thus reinforce a female's oviposition decision when the image of ants is also present. This hypothesis can be related to the fact that *G. xiphias* aggregations increase the number and predictability of mutualistic ants in time and space (Del-Claro & Oliveira, 1996).

For myrmecophilous butterflies, facultative interactions are more common in nature, yet most studies focus on the more specialised, obligate associations (Pierce *et al.*, 2002). Although the occurrence of *P. polibetes* eggs on a plant is not conditioned by ant presence on leaves, butterfly females do prefer to lay eggs in proximity to ants, as also shown for another facultatively myrmecophilous lycaenid butterfly, *Hemiargus isola* Reakirt (Wagner & Kurina, 1997). However, given the different degrees of specialisation in the interaction between myrmecophilous caterpillars and ants, it is possible that the nature of the cues utilised by ovipositing females depends on the degree of the association with tending ants (Fraser *et al.*, 2002; Pierce *et al.*, 2002). As a result, one would expect that cues would be more generalised in facultative than in obligate associations, because in the former case the caterpillar can be tended by several ant species (16 ant species in three subfamilies have been recorded tending *P. polibetes* caterpillars; see Oliveira & Del-Claro, 2005; Kaminski *et al.*, 2012).

To our knowledge, this is the first study to demonstrate experimentally the separate role of ants and of ant–treehopper

associations as visual cues for egg-laying myrmecophilous butterflies. However, it does not discard the possibility that ovipositing *P. polibetes* females may use additional cues other than visual to detect ants and treehoppers on foliage. Chemical compounds are usually of great importance for host plant selection in lepidopterans (Chew & Robbins, 1984; Thompson & Pellmyr, 1991) and may be relevant in the *P. polibetes*–ant–treehopper–*S. vinosa* system as well. Indeed, the cues used by myrmecophilous butterflies clearly deserve further investigation, and a great knowledge about this matter will certainly bring new insights about the evolution and functioning of myrmecophily in Lepidoptera. Our results indicate that facultative ant–caterpillar mutualistic interactions can shape behavioural traits in adult butterflies of myrmecophilous species: the search for a safe, ant-occupied place for offspring development seems crucial for this insect group. More generally, our research shows that facultative mutualisms can be important enough to promote a behavioural adaptation (visual discrimination) reinforcing the interaction. Our study highlights the behavioural interface within complex multispecies systems, as illustrated by this ant-based mutualism involving exudate-producing treehoppers and caterpillars.

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