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Ant-lepidopteran associations along African forest edges

Alain Dejean[1,2] · Frédéric Azémar[1] · Michel Libert[3] · Arthur Compin[1] ·
Bruno Hérault[2] · Jérôme Orivel[2] · Thierry Bouyer[4] · Bruno Corbara[5,6]

Abstract Working along forest edges, we aimed to determine how some caterpillars can co-exist with territorially dominant arboreal ants (TDAAs) in tropical Africa. We recorded caterpillars from 22 lepidopteran species living in the presence of five TDAA species. Among the defoliator and/or nectarivorous caterpillars that live on tree foliage, the Pyralidae and Nymphalidae use their silk to protect themselves from ant attacks. The Notodontidae and lycaenid Polyommatinae and Theclinae live in direct contact with ants; the Theclinae even reward ants with abundant secretions from their Newcomer gland. Lichen feeders (lycaenid; Poritiinae), protected by long bristles, also live among ants. Some lycaenid Miletinae caterpillars feed on ant-attended membracids, including in the shelters where the ants attend them; *Lachnocnema* caterpillars use their forelegs to obtain trophallaxis from their host ants. Caterpillars from other species live inside weaver ant nests. Those of the genus *Euliphyra* (Miletinae) feed on ant prey and brood and can obtain trophallaxis, while those from an Eberidae species only prey on host ant eggs. *Eublemma albifascia* (Erebidae) caterpillars use their thoracic legs to obtain trophallaxis and trophic eggs from ants. Through transfer bioassays of last instars, we noted that herbivorous caterpillars living in contact with ants were always accepted by alien conspecific ants; this is likely due to an intrinsic appeasing odor. Yet, caterpillars living in ant shelters or ant nests probably acquire cues from their host colonies because they were considered aliens and killed. We conclude that co-evolution with ants occurred similarly in the Heterocera and Rhopalocera.

✉ Alain Dejean
   alain.dejean@wanadoo.fr

1   Ecolab, Université de Toulouse, CNRS, INPT, UPS, UPS-ECOLAB, 118 route de Narbonne, 31062 Toulouse, France

2   CNRS, UMR EcoFoG, AgroParisTech, Cirad, INRA, Université des Antilles, Université de Guyane, 97310 Kourou, France

3   8 rue Henry Barbet, 76000 Rouen, France

4   57 rue Genot, 4032 Chênée, Belgium

5   CNRS, UMR Laboratoire Microorganismes, Génome et Environnement, Université Blaise Pascal, Complexe Scientifique des Cézeaux, 63177 Aubière Cedex, France

6   Université Clermont Auvergne, Université Blaise Pascal (LMGE), 63000 Clermont-Ferrand, France

Introduction

Among insects, the extreme diversity of the order Lepidoptera (≈160,000 species described; 500,000 estimated species) is related to the rise of angiosperms as the larvae of most species are exclusively phytophagous and each generally associated with only a few plant families (Foottit and Adler 2009). Yet, the caterpillars of 200–300 known lepidopteran species are aphytophagous, feeding on lichens, keratin, and insects (mostly Hemipterans) or are parasites in ant nests (Pierce 1995).

Over the course of evolution, caterpillars came into increasing contact with ants that hold a keystone position in most terrestrial ecosystems and generally prey on any eggs or first

instar larvae they find on plants. This is particularly the case in the tropics where rainforest canopies are occupied by territorially dominant arboreal ants (TDAAs). These ants have very populous colonies; they build large or polydomous nests (i.e., carton builders, carpenter ants, weaver ants); are strong predators; and are territorial toward other TDAAs, creating what has become known as "arboreal ant mosaics" (Dejean et al. 2007, 2015). Yet, certain caterpillars have evolved a range of mechanisms to overcome this predation pressure by deterring ants using repellent or sticky regurgitations (DeVries 1991; Rosta and Blassmann 2009), having long hair that can bear venom glands (Smedley et al. 2002), or living in a group and building shelters using their silk (Young 1986; Fitzgerald 1996; Roux et al. 2011).

For other lepidopterans, most of them belonging to the family Lycaenidae, the caterpillars have several ways of being accepted by ants (Pierce et al. 2002). Indeed, despite the fact that ants recognize their kin through their cuticular hydrocarbons (CHCs), numerous invertebrates called myrmecophiles have evolved adaptations to live in association with ants based on the following: (1) a cuticular profile matching that of their host ants through biosynthesis (chemical mimicry) or acquisition (chemical camouflage); (2) a low quantity of CHCs (chemical insignificance); (3) compounds attractive to the ants (e.g., biosynthesized or acquired from ant-attended hemipterans); (4) a food reward (associated or not with the previous cases); and/or (5) the use of defensive strategies (Lenoir et al. 2001).

Because TDAA workers spread-eagle both enemies and prey and do not necessarily use their venom, they can master large arthropods (Dejean et al. 2007) so that the morphological protections of lycaenid caterpillars, such as a thick cuticle or specialized setae (Dupont et al. 2016), are futile without a supplementary chemical arsenal. These caterpillars can live on plant foliage where they are tolerated or protected by ants when they are herbivores, nectarivores, exploiters of the honeydew of ant-attended hemipterans, or when they prey on the latter. On the other hand, they can be parasites, living in ant nests where they prey on the brood or are fed through regurgitations or trophallaxis (cuckoo parasites) (Pierce et al. 2002).

In addition to possible similarities in their CHC profiles with those of their host ants through mimicry or camouflage, compounds from several glands facilitate the acceptance of lycaenid caterpillars by ants. The pore copula organs, generally distributed over a large part of the caterpillars' cuticle, are likely present in all lycaenids. They produce compounds inhibiting ant aggressiveness and can also secrete amino acids as a food reward (Atsttat 1981; Pierce et al. 2002; Dupont et al. 2016). The Newcomer gland, which produces a food reward for ants in the form of sugars and amino acids, is present in the caterpillars of most Curetinae, Theclinae, Polyommatinae, and Lycaeninae (Pierce et al. 2002; Daniels et al. 2005).

These lycaenid taxa also possess tentacle organs which secrete volatiles that attract and alert ants. Other glands have also been noted in interactions with ants. For the Miletinae, the caterpillars, which are insect predators or ant parasites, lack the Newcomer gland, but those of the genus *Aslauga* have tentacle organs. So, their interactions with ants depend primarily on CHCs and pore copula organs (Pierce et al. 2002; Kaliszewska et al. 2015).

We hypothesized that we could record several means by which caterpillars resist TDAA aggressiveness by monitoring the most frequent plant species developing along forest edges in tropical Africa: the extrafloral nectar-bearing Euphorbiaceae *Alchornea cordifolia*. Indeed, compared to the forest canopy, the vegetal formations lining forest edges are low enough to permit direct observations (Dejean and Gibernau 2000). Our threefold aim was to (1) determine if a specialized association exists between caterpillars and TDAAs; (2) verify if caterpillars from certain lepidopteran species can be found on other tree species; and (3) establish if among those caterpillars living in contact with TDAAs, and so able to inhibit their aggressiveness, there is a fundamental difference between those living in the host plant foliage and those living in close contact with workers in shelters or as parasites in ant nests.

Materials and methods

Study area and focal plant species

Field studies were conducted in Cameroon at different sites situated within a radius of ≈80 km around the city of Yaoundé (03° 52′ N, 11° 31′ E).

Alchornea cordifolia (Euphorbiaceae) is a common sarmentous shrub that grows up to 8 m tall in riparian areas and humid zones along dirt roads that crisscross forests. As the shoots grow, they generally bend, become horizontal, and end up by touching the ground where they take root, producing a network of branches and forming patches extending over zones of up to 150 m along forest edges. The alternate leaves have a 5–15-cm-long petiole and an ovate, acuminate lamina (10–25 cm × 7–15 cm) bearing four patches of extrafloral nectaries (EFN) at the base of the underside of the lamina. Unisexual flowers can be borne by either male or female inflorescences and the fruits are two-seeded capsules (Dejean and Gibernau 2000; Mavar-Manga et al. 2007).

Protocol of the study

To obtain a representative sample of the ant species occupying their foliage, we selected 130 *A. cordifolia* patches 50–100 m in length along forest edges (Table 1). We also looked for

caterpillars associated with these ant species regardless of the tree species (one to four researchers inspecting each tree and opening the ant nests; 6 km of forest edge inspected in total; 140 plants closely examined; Table 1).

We recorded the following ant species able to occupy an entire *A. cordifolia* patch. *Crematogaster striatula* (Myrmicinae) nests in rotting branches, most of them lying on the ground; the workers forage on the adjacent tree foliage. *Oecophylla longinoda* (Formicinae) workers construct multiple nests by manipulating ant larvae as shuttles, using the silk they produce to bind some host tree leaves together (weaver ants). *Tetramorium aculeatum* (Myrmicinae) workers build carton nests under the leaves of their host trees. *Camponotus brutus* (Formicinae) has the same nesting and foraging modes as *C. striatula* with which it can be associated. *Myrmicaria opaciventris* (Myrmicinae) is a ground-nesting species whose nests are interconnected by galleries; workers can forage on small trees (Dejean et al. 2007).

We looked for defoliator and nectarivorous caterpillars by thoroughly inspecting the foliage of each selected plant and then we opened the shelters where the ants attended hemipterans as well as the ant nests to note if they sheltered caterpillars.

Laboratory-bred colonies for observation and to obtain adult Lepidoptera

The caterpillars observed on plant foliage were gathered along with the branches on which they were found and 30–50 ant workers. The whole was put into large, transparent plastic bags and transported to the laboratory where the bases of the branches were placed into a vase containing water. A piece of cotton was set above the water between the bases of the branches to prevent the caterpillars from falling into the water. The mouth of the plastic bag was fit to the upper part of the vase using a rubber band.

When caterpillars were found inside the ant nests, we collected the latter by cutting down the supporting branches using a clipping pole for *O. longinoda* or gathering the rotting logs in which *C. brutus* or *C. striatula* sheltered, put them into plastic bags, and took them to the laboratory. The large, terrestrial *M. opaciventris* nests were studied only in the field. Collected nests were installed in 40 × 20 × 5 cm plastic boxes with a transparent cover (which we covered with a screen outside of observational periods to keep the artificial nest in the dark) opening onto a table through holes 0.8 cm in diameter permitting the passage of emerging adult Lepidoptera whose wings are still folded. Slats of wood were placed between the tables and planters containing *A. cordifolia* (1.5–2 m in height) to permit the workers to forage for extrafloral nectar and honeydew as they attended hemipterans on these plants (the bases of the legs of the tables

and the planters were placed in canisters filled with oil to prevent the ants from escaping). The ants were provided ad libitum with water, honey, and prey (mostly cricket larvae and mealworms). The interactions between the ants and the caterpillars were filmed, including inside artificial nests (see Collet 1996, 2004).

Confrontation experiments

Ant workers distinguish colony mates from aliens based on low-volatile cuticular hydrocarbons (CHCs) whose primary function is to protect insects from desiccation. During self- and allogrooming, trophallaxis, and inter-individual contact, the workers continually gather their own CHCs and those of their colony mates in the postpharyngeal gland where they homogenize them into a mixture that they spread onto their own cuticle. This process results in the formation of the "colony odor" that changes over time because, in addition to the synthesized CHCs, it is influenced by compounds from the diet, nesting material, and associated microorganisms. The colony odor is learned by each worker for which it constitutes a "template" that is compared to the cues received through antennation when encountering other individuals (d'Ettorre and Lenoir 2010).

The combination of synthesized CHCs constituting the colony odor varies between species, while conspecific colonies share the same blend of CHCs but at different concentrations, something bolstered by the CHCs acquired from the environment (Van Wilgenburg et al. 2011).

Due to within-colony variation in CHCs (e.g., differences between castes, acquisition of CHCs from the environment), a threshold exists permitting colony mates to be admitted while hetero- or conspecific aliens are aggressively rejected (d'Ettorre and Lenoir 2010; see also Leclerc and Detrain 2016). The territorial threshold of acceptance between TDAA species is very high intra- and interspecifically, resulting in the mosaic pattern distribution of their territories in tropical rainforest (Dejean et al. 2015). Non-dominant species are tolerated on their territories but are attacked and eaten during periods of dearth (Dejean et al. 2007), and the caterpillars of some lepidopteran species have been noted inside TDAA nests (Dejean et al. 2016). These facts show that there are different thresholds of tolerance by TDAAs. In ants, heterospecific inter-individual contact is enough to modify the chemical profile of workers, triggering the killing of colony mates (Dejean and Corbara 2014; Dejean et al. 2014), something chemically demonstrated through experimental methods of CHC transfer (Roux et al. 2009, 2013). So, we hypothesized that caterpillars living in direct contact with TDAAs as parasites in shelters or in nests during their entire larval life can acquire CHCs from the ants (chemical camouflage; Akino 2008). If so, these caterpillars will be attacked if transferred to another conspecific colony as are ant workers in

Table 1 Tripartite associations between *Alchornea cordifolia*, the five dominant ant species noted in the area studied and Lepidoptera. The family is provided for non-lycaenid species, and the subfamily is provided for the Lycaenidae. "patches": patches of *A. cordifolia* individuals (branches intermingled over 50–100 m along forest edges) corresponding to the territory of an ant colony; under "patch." are presented the number of cases when we noted the presence of caterpillars; "cater.": number of caterpillars observed. (Por.): (Poritiinae); (Polyomm.): (Polyommatinae); (Milet.): (Miletinae). Asterisk up to 359 caterpillars (see Dejean et al. 2016)

Ant species	Caterpillars living on the foliage of *Alchornea cordifolia* (Euphorbiaceae)										Alternative plants (or information on caterpillar feeding habits)
	Crematogaster striatula (30 patches)		*Oecophylla longinoda* (30 patches)		*Tetramorium aculeatum* (30 patches)		*Camponotus brutus* (30 patches)		*Myrmicaria opaciventris* (10 patches)		
Lepidoptera species	patch.	cater.	patch.	cater.	patch.	cater.	patch.	cater.	patch.	cater.	
Pyralinae sp.1 (Pyralidae)	4	36									
Neptis serena (Nymphalidae)	1	3									*Abizia zygia* (Fabaceae): 3 saplings/19; 8 caterpillars *Cycinia* sp. (Euphorbiaceae); Williams (2008–2016)
Triclema lamias (Polyommatinae)	6	>40									Gather honeydew from a Coccidae; Farquharson (1921)
Triclema fasciatus (Polyomm.)	1	4									
Triclema josianae (Polyomm.)	4	30									
Aphnaeus orcas (Theclinae)	6	21									Also noted on *Trema* spp. (Ulmaceae) at Ndūpe (3° 53′ N, 10° 41′ E; AD pers. obs); Anacardiaceae, Euphorbiaceae, Fabaceae, Flacourtiaceae, Loranthaceae, Oleaceae, Rhamnaceae, Rubiaceae and Sapindaceae; Williams (2008–2016)
Virachola antalus (Theclinae)	1	6									Also noted on Fabaceae, Combretaceae, Oleaceae, Rosaceae, Sapindaceae and Solanaceae; Williams (2008-2016)
Lachnocnema sp. (Miletinae)	1	12									Feed on membracid honeydew or prey on them
Pyralinae sp.2 (Pyralidae)			1	18							Also noted on *A. cordifolia* at Matomb (3° 53′ N, 11° 4′ E; AD pers. obs)
Notodontidae sp. 1			1	1							Also noted on *A. cordifolia* at Akok (2° 38′ N, 9° 53′ E; AD pers. obs)
Dapidodigma demeter (Theclinae)			7	>40							On *Albizia* sp. (Fabaceae); *Homalium* sp. (Flacourtiaceae); Williams (2008–2016)
Hewitsonia danane (Poritiinae)			1	1							Lichen feeder; noted on *Citrus* (Rutaceae): 4 trees/30; 9 caterpillars
Cephetola mercedes dejeani (Poritiinae)			1	6							Lichen feeder; also noted at Ndūpe (3° 53′ N, 10° 41′ E; AD pers. obs)
Neurellipes lusones (Polyomm.)					1	3					Also noted on *A. cordifolia* at Akok (2° 38′ N, 9° 53′ E; AD pers. obs)
Caterpillars living in shelters where the ants attend hemipterans											
Aslauga vininga (Miletinae)	2	5									Zingiberaceae: 3 trees/40; 6 caterpillars
Lachnocnema emperamus (Miletinae)							2	16	1	6	*Bridelia micrantha* (Phyllanthaceae): 3 trees/15; 17 caterpillars also *Myrmicaria opaciventris*: 2 trees/10; 11 caterpillar *Macaranga* spp. (Euphorbiaceae): 8 trees/21; >40 caterpillars
Lachnocnema magna (Miletinae)							2	5			*Bridelia micrantha* (Phyllanthaceae): 2 trees/15; 6 caterpillars
Caterpillars living inside *Oecophylla longinoda* nests											
			4	12							Also noted in orchards (citrus, mango, and guava trees; AD pers. obs)

Table 1 (continued)

Ant species	Caterpillars living on the foliage of *Alchornea cordifolia* (Euphorbiaceae)										Alternative plants (or information on caterpillar feeding habits)
	Crematogaster striatula (30 patches)		*Oecophylla longinoda* (30 patches)		*Tetramorium aculeatum* (30 patches)		*Camponotus brutus* (30 patches)		*Myrmicaria opaciventris* (10 patches)		
Lepidoptera species	patch.	cater.	patch.	cater.	patch.	cater.	patch.	cater.	patch.	cater.	
Euliphyra cameruna (Miletinae)											
Euliphyra leucyania (Miletinae)			4	18							Also noted in orchards (citrus, mango, and guava trees; AD pers. obs)
Pyralinae sp.3 (Pyralidae)			1	1							
Wurthiinae sp.1 (Crambidae)			1	2							
Eublemma albifascia (Erebidae; Boletobiinae)			4	>200*							Also noted in orchards (citrus, mango, and guava trees; AD pers. obs)

this situation, while this process is unlikely for caterpillars living on the host plant foliage as herbivores and rather relying on other means of being accepted.

In keeping with the idea that simple, practical research approaches are needed to study the basic biology of insects (Tschinkel 2011), we conducted an experiment based on transferring the caterpillars of the most frequent species. The controls consisted in transferring caterpillars from the part of the host *A. cordifolia* where they were gathered to a place occupied by the same ant colony (same territory; same *A. cordifolia* patch) situated 25–30 m away (≈15 m for *C. brutus* whose territories are smaller). 'Experimental' caterpillars were transferred from one *A. cordifolia* patch to another sheltering a conspecific, alien colony situated more than 200 m away. Among herbivorous caterpillars living on the *A. cordifolia* foliage, we tested 20 *Aphnaeus orcas* caterpillars living on *C. striatula* territories and 25 *Dapidodigma demeter* caterpillars living on *O. longinoda* territories (these Theclinae caterpillars have active Newcomer glands). We also tested 16 *Lachnocnema emperamus* caterpillars (Miletinae) in shelters where *C. brutus* were attending hemipterans. Finally, among the parasitic caterpillars living in *O. longinoda* nests, we tested 25 *Euliphyra leucyania* caterpillars (Miletinae) and 30 *Eublemma albifascia* (Erebidae; Boletobiinae) (half of these totals indicate the control lots, the other half refers to the experimental lot).

For verification, the same protocol was conducted using ant workers ($N = 30$ in each case). During their transfer, to avoid polluting their cuticle, the ants and caterpillars were kept on the leaves on which they were found; these leaves were then placed in a carton box. Workers were installed in a new area by pushing them with thin, clean forceps; they were rarely seized during this process. The caterpillars were seized using smooth, clean forceps and placed very gently in the new area.

Comparison between two groups in three situations or comparisons between these situations were made using Fisher's exact test and the false discovery rate adjustment for simultaneous comparisons, BH correction (Pike 2011).

Results and discussion

We recorded five ant species able to occupy all of the foliage in *A. cordifolia* patches and caterpillars from 22 lepidopteran species and morphospecies able to live in their presence. This corresponds to seven lepidopteran families including the Rhopalocera (Lycaenidae and Nymphalidae) and the heterocera (Erebidae, Notodontidae, and Pyralidae) (Table 1; see a selection of adults in Fig. 1).

The caterpillars can be divided into three main groups depending on where they develop: (1) on the host *A. cordifolia* foliage (i.e., defoliators, nectarivores, lichen feeders, exploiters of membracids), (2) inside the shelters built by the ants to attend hemipterans, or (3) inside the ant nest (all parasites of *O. longinoda* colonies) (Table 1).

Lachnocnema emperamus caterpillars that develop either in association with *C. brutus* or *M. opaciventris* colonies are exceptions with regard to the interactions between lepidopteran and TDAA species that were specific in other cases (Table 1; see below the rare exceptions of caterpillars noted with congeneric TDAAs). We also noted a specificity between the defoliator and/or nectarivorous caterpillars of seven lepidopteran species

Fig. 1 Adults of the different Lepidoptera species studied. The *horizontal bars* represent 10 mm

and their host plant (i.e., *A. cordifolia*), while four others are notably polyphagous (Table 1). The first case reflects the fact that phytophagous caterpillars are generally specialized (Foottit and Adler 2009); the second is in keeping with the idea that associations with ants broaden their host plant range (Fiedler 1994; Forister et al. 2011).

Note that experimental studies have shown that ants protect lycaenid caterpillars, even facultative myrmecophilous ones, living on the same host plant foliage from predators and parasitoids; this is known as "enemy-free space" (see Atsatt 1981; Pierce 2002). So, caterpillars living on the TDAAs' territories likely benefit from protection.

Defoliator caterpillars able to resist ant predation pressure: the protective role of silk

Secreted from glands located on different parts of arthropods, silk is extruded as a liquid via a nozzle-like apparatus and then forms a thread of fibrous protein. It is used in the construction of different structures such as spider webs, moth cocoons, weaver ant nests, and the silken shelters made by caterpillars of the Yponomeutidae and Lasiocampidae (Roessingh 1990; Fitzgerald 1996).

Among the heterocera, Pyralinae sp.1 caterpillars feed on young leaves growing at the extremities of branches and isolate themselves from *C. striatula* worker attacks

thanks to strands of silk that they string between these branches (Table 1; Fig. 2a). Similarly, the caterpillars of a Neotropical Pyralidae protect themselves from *Azteca* ant attacks using strands of silk (Roux et al. 2011). Also, groups of Pyralinae sp.2 caterpillars build nests by binding the host plant leaves together with their silk, thus roughly imitating the *O. longinoda* nests distributed throughout the rest of the foliage (Table 1). They leave their nests nocturnally to feed on the host plant foliage when the *O. longinoda* workers are less active (Dejean et al. 2007) and immediately take refuge in their nest once the workers begin to attack them (see Supplementary movie 1 for additional details). This behavior is similar to that of *Brassolis* caterpillars (Nymphalidae) which forage at night and group together inside their silk-bound shelters during the daytime (Young 1986; see Herbison-Evans and Crossley 2016 for a similar cases in another Pyraline).

Among the Rhopalocera, *Neptis serena* caterpillars (Nymphalidae), which have been noted on several plant species (Table 1), place strands of silk on the petiole of the leaf which they then consume; this silk is sufficient to protect them from *C. striatula* worker attacks as the latter never try to cross this barrier. Last-stage caterpillars cut strips of leaves up to the main vein, the remaining parts of the lamina end up by drying out and turning yellowish; here, too, the caterpillars deposit strands of silk along the upper part of the main vein to prevent *C. striatula* workers from passing (see Supplementary movie 2 for additional details). Pupation occurs at the extremity of the main vein; the pupae, mimetic of the dried pieces of lamina, are protected from bird attacks (Fig. 2).

Therefore, although used for different structures, the silk of all these caterpillars permits the latter to live in the presence of both *O. longinoda* and *C. striatula* colonies by diverting the workers which are strong predators (Dejean et al. 2007; Rifflet et al. 2011).

Defoliator and/or nectarivorous caterpillars living in contact with the ants

Among the heterocera, Notodontidae sp.1 caterpillars feed both on young *A. cordifolia* leaves and on EFN and try to obtain regurgitations from *O. longinoda* workers by using their hypertrophied forelegs (Table 1; Fig. 2).

Among the Rhopalocera, *Triclema lamias*, *Triclema fasciatus*, and *Triclema josianae* caterpillars (Lycaenidae; Polyommatinae) live in association with *C. striatula* at the extremities of twigs (Table 1). *T. lamias* caterpillars are both nectarivorous and defoliators of very young leaves; their impact is easy to observe on older leaves (Fig. 2; see also Jackson 1947). They

were also observed gathering honeydew from scale insects (Farquharson 1921). *T.fasciatus* and *T. josianae* caterpillars are strict nectarivores (Fig. 2) (see also Libert 2010). *Neurellipes lusones* caterpillars (Polyommatinae), associated with *T. aculeatum*, feed on young *A. cordifolia* leaves and on EFN (Table 1) (see also Libert 2010). They likely have a Newcomer gland because the ants licked their posterior parts as noted for *Triclema* spp.; certain of them also have tentacle organs (Fiedler 1991).

Defoliator and/or nectarivorous caterpillars providing a food reward to ants

Aphnaeus orcas caterpillars (Lycaenidae; Theclinae) are always surrounded by *C. striatula* workers and even transport them. Their Newcomer gland is hypertrophied and not eversible, seemingly a "drinking trough" (Table 1; Fig. 3a), while the two tentacle organs are very frequently active (Collet 1996, 2004). These caterpillars, which can also feed on EFN, are euryphagous, feeding on several plant species belonging to different families (Table 1). This is also the case for *Virachola antalus* caterpillars associated with *C. striatula* (Table 1). Note that *Aphnaeus adamsi* caterpillars can engage in trophallaxis with their host *Crematogaster* sp. ants (Callaghan 1993; Fiedler 2012).

Caterpillars of another Theclinae, *D. demeter*, are defoliators associated with *O. longinoda* (Fig. 3b). They were also found on a Fabaceae and a Flacourtiaceae (Table 1). One can see a similarity with the associations between the Asian weaver ant *Oecophylla smaragdina* and different Theclinae caterpillars of the genera *Anthene* and *Hypolycaena*, but the latter begin their life cycle inside ant nests where they are transported by workers (Fiedler and Maschwitz 1989; Moss 1989; Tokeshi et al. 2007).

Lichen-feeding caterpillars living in contact with the ants and protected by long hairs

Both *Hewitsonia danane* and *Cephetola mercedes dejeani* caterpillars (Lycaenidae; Poritiinae) are lichen feeders found on plants occupied by *O. longinoda* colonies but are protected by long bristles (Table 1; Fig. 2; Callaghan 1992; Libert 1999). They likely feed only on the algal part of the lichens (Bampton 1995) but might also feed on Cyanophyta (Bouyer 1997).

Caterpillars exploiting ant-attended hemipterans (on the host plant foliage or inside shelters built by the ants)

Lachnocnema sp.1 caterpillars (Lycaenidae; Miletinae) live in a group on host plant twigs on which they exploit the honeydew of membracids attended by *C. striatula* and prey on

these membracids (Table 1; Fig. 3). *Aslauga vininga*, also associated with *C. striatula*, prey on scale insects attended by this ant species (Table 1; Fig. 3; see also Lamborn 1914 who noted that the caterpillars were associated with another *Crematogaster* species).

Lachnocnema emperamus caterpillars, which can be associated with *M. opaciventris* (Myrmicinae) or *C. brutus* (Formicinae) colonies attending *Leptocentrus* sp. (Membracidae) nymphs in shelters situated at the base of trees, feed on the honeydew of the membracids, prey on them and trigger trophallaxis from ant workers (Table 1); they also feed on Psyllidae (Seth-Smith 1938). Adult *L. emperamus* individuals, their legs protected by long hairs (Fig. 3), feed on the honeydew produced by ant-attended scale insects, the females laying their eggs while in contact with the ants. So, there is a strong similarity with *Lachnocnema bibulus* (absent from Cameroon). In Kenya, *L. bibulus* caterpillars feed on membracid and jassid honeydew, prey on them, and are able to trigger trophallaxis from their host ants (not identified) which transport just-hatched caterpillars to the shelters where they attend hemipterans (Cripps and Jackson 1940; Clark and Dickson 1971).

Lachnocnema magna caterpillars were only found in association with *C. brutus* in this study. They also feed on the honeydew of *Leptocentrus* sp. membracids, prey on them and trigger trophallaxis from workers, something facilitated by their hypertrophied forelegs (Table 1; Fig. 3). The frequency of trophallaxis was particularly high, especially for last instar individuals.

Devoid of a Newcomer gland, Miletinae caterpillars are aphytophagous, most of them feeding on sap-sucking hemipterans attended by ants; this condition is considered plesiomorphic in this subfamily (Pierce 1995; Pierce et al. 2002; Boyle et al. 2015; Kaliszewska et al. 2015). Indeed, a shift occurred for the caterpillars of some Miletinae that are able to live in ant nests becoming predators of their brood and triggering regurgitations (Pierce et al. 2002).

Parasitic caterpillars living inside ant nests

Among the heterocera, the only Pyralinae sp.3 individual observed in this study was a pre-pupa, so that we never saw it feeding.

Wurthiinae sp.1 caterpillars, which are protected by curly hairs, feed voraciously on *O. longinoda* eggs (Fig. 3; see Supplementary movie 3 for additional details). Note that the subfamily Wurthinae (Pyraloidea; Crambidae) comprises the only Indo-Australian genus *Niphopyralis* (formerly *Wurthia*) with eight known species which likely feed on ant brood (Kemner 1923; Robinson et al. 1994; Pierce 1995). Moreover, our case converges with that of *Niphopyralis myrmecophila* caterpillars from Java which feed on the brood of congeneric *O. smaragdina* (Roepke 1916). The discovery

of a member of this subfamily in Africa is new, to the best of our knowledge, which led to further study (Maes KVN, TB, AD, pers. com.). In accordance with Solis and Maes (2002), Regier et al. (2012) included the Wurthinae in the Spilomelinae based on molecular data.

We also noted the presence of *E. albifascia* caterpillars in four patches of *A. cordifolia* each sheltering an *O. longinoda* colony (Table 1). The parasitized colonies sheltered 359 caterpillars which obtained trophallaxis (Fig. 3; see Supplementary movie 4 for additional details) and trophic eggs, so that the *O. longinoda* queen was starved, stopped laying eggs, and died (Dejean et al. 2016). Adult *E. albifascia* females oviposit in the proximity of *O. longinoda* nests and just-hatched caterpillars trick the workers into transporting them to their nest (Dejean et al. 2016). Note that the caterpillars of most *Eublemma* species are specialized coccid predators (Pierce 1995; Vu et al. 2006). This is in keeping with the suggestion that the ability to prey on sap-sucking hemipterans is one of the prerequisites in the evolution toward myrmecophily (Fiedler 2012). Indeed, *Eublemma scitula* and *Eublemma ochrochroa* caterpillars can move freely among ants attending scale insects; *E. ochrochroa* caterpillars use their silk to keep the remains of scale insects on their body to lure the ants like "wolves in sheeps' clothing" (Lamborn 1914; Panis 1974). Also, *Cyclotorna monocentra* (Cyclotornidae) caterpillars first parasitize Cicadellidae before moving into the nests of the dolichoderine ant *Iridomyrmex purpureus* where they consume the brood (Dodd 1912; Pierce 1995).

Concerning the Rhopalocera, miletine *Euliphyra mirifica* caterpillar interactions with *O. longinoda* were first described by Lamborn (1914; see details in Williams 2008–2016 File N) who noted that they can steal honeydew during trophallaxis between workers and trigger regurgitations from an ant donor; they can also follow host ant trails (Dejean and Beugnon 1996). We noted that *E. cameruna* and *E. leucyania* caterpillars did the same and can also feed on prey retrieved by hunting workers and sometimes on brood (Table 1; Fig. 3) (see Libert 2016 for a recent revision of the Liphyrini). Also, adult females of both species oviposit on trees sheltering an *O. longinoda* colony, even on the leaves composing their nests.

Regarding *Euliphyra* caterpillars, triggering regurgitations by host ants result from a simple contact with their labium as has been noted for other miletine caterpillars (Pierce et al. 2002). This contact is sufficient because in ants the antennation of the donor head is enough for trophallaxis to occur. So, the evolutive process took place only on the myrmecophile side, without apparent parallel evolution on the ant side (Passera and Aron 2005). One can note a similarity between these *Euliphyra* caterpillars and those of the Indo-Australian species *Liphyra brassolis* and its associate ant *O. smaragdina* (Samson and Smart 1980; Kaliszewska et al. 2015). Protected by a hard covering, these flat, oval caterpillars live in ant nests where they feed only on the brood (Parsons 1999).
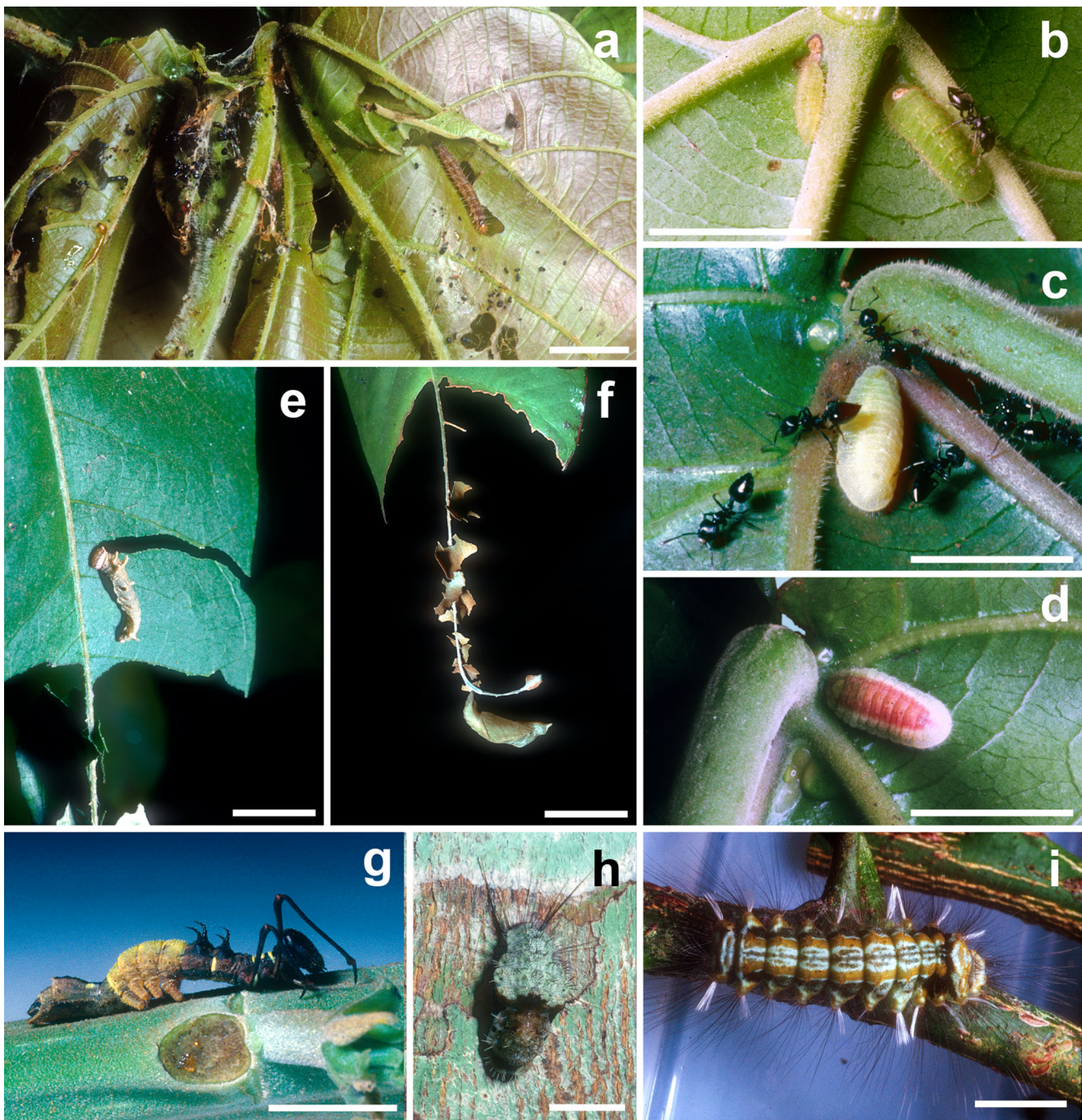
Fig. 2 The different defoliator and/or nectarivorous caterpillars studied. **a** Pyralinae sp.1 caterpillars feed on young *Achornea cordifolia* leaves and spin strands of silk to protect themselves from *Crematogaster striatula* workers. **b–d** *Triclema lamias* caterpillars are both defoliator and nectarivorous while *T. fasciatus* and *T. josianae* caterpillars feed only on extrafloral nectar. **e**, **f** Type of defoliation by *Neptis serena* caterpillars leaving strips of leaves that will dry out and then serve as camouflage for the pupae. **g** A Notodontidae sp.1 caterpillar; they feed on young leaves while their hypertrophied forelegs permit them to obtain trophallaxis from *Oecophylla longinoda* workers. **h**. **i** A pupa (mimetic of the substratum) and a *Hewitsonia danane* caterpillar; these caterpillars are lichen feeders which develop and pupate among foraging *O. longinoda* workers. The *horizontal bars* represent 10 mm

Caterpillar acceptance by ants

The examinations conducted using ant workers resulted in a law of all or nothing. The transfer between two distant areas of one territory always resulted in the acceptance of the introduced individuals. The same was true for all of the caterpillars tested.

The transfer of workers between the territories of two conspecific colonies (same host plant species: *A. cordifolia*),
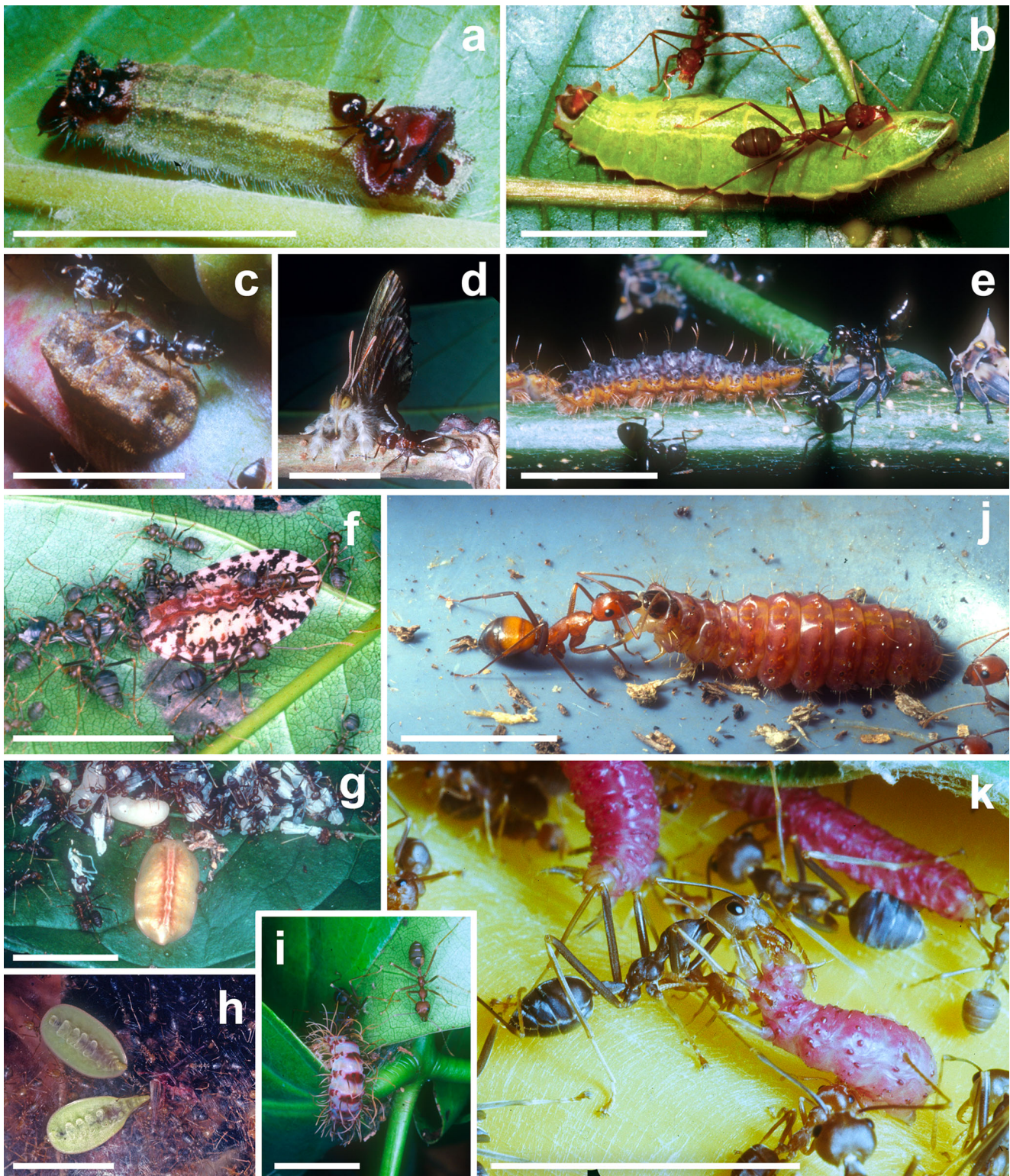
resulted in the killing of introduced, aliens individuals, while all caterpillars living on the host plant foliage were accepted and 21.42 % of those living in ant nests survived the transfer (significant difference with ant transfer in both cases; Fig. 4).

Transferring caterpillars from one part of an *A. cordifolia* patch to another occupied by workers from the same colony versus transferring them from one patch to another sheltering an alien conspecific colony resulted in a non-significant difference for herbivorous caterpillars living on plant foliage (Fig. 4). Indeed, no caterpillars were killed; we only noted some aggressive reactions in the second situation. Yet, the difference was significant for caterpillars living in ant shelters

◄ **Fig. 3** Caterpillars with different feeding modes including those living in ant shelters or ant nests. **a** A defoliator and nectarivorous *Aphnaeus orcas* caterpillar transporting a *Crematogaster striatula* worker feeding on its drinking trough-shaped Newcomer gland. **b** A defoliator *Dapidodigma demeter* caterpillar with an *Oecophylla longinoda* worker imbibing secretions from its Newcomer gland. **c** An *Aslauga vininga* caterpillar mimetic of the shelter made by *C. striatula* workers to tend coccids; the caterpillars feed on these coccids although surrounded by ants. **d** *Lachnocnema emperamus* butterfly with its hairy legs permitting it to settle among *Myrmicaria opaciventris* workers. **e** *Lachnocnema* sp. 1 caterpillars preparing to attack membracids attended by *C. striatula* workers. **f**, **g** *Euliphyra leucyania*; a caterpillar in a just-opened *O. longinoda* nest, two others feeding on a prey. **h** A *Euliphyra cameruna* caterpillar in an *O. longinoda* nest. **i** A Wurthiinae sp1 caterpillar. **j** Trophallaxis between a *Lachnocnema magna* caterpillar and a *Camponotus brutus* worker. **k** Trophallaxis between an *Eublemma albifascia* caterpillar and an *O. longinoda* worker. The *horizontal bars* represent 10 mm

or in ant nests (all of the caterpillars were attacked, 78.57 % were killed when transferred to the territory of another conspecific ant colony; the survivors belonged to both species tested Fig. 4). The first case (i.e., caterpillars living on plant foliage) was also significantly different from the two others (i.e., caterpillars living in ant shelters or in ant nests), which were not different from each other (Fig. 4).

It is likely that, to be accepted by ants, caterpillars living on plant foliage rely rather on compounds from their pore copula organs plus their Newcomer gland, so that their transfer ends in their adoption. Caterpillars living in close contact with ants likely acquire CHCs from the latter (chemical camouflage), so that conspecific, heterocolonial ants consider them aliens and

attack, killing most of them. The significant difference noted with the transfer of ant workers between the territories of two *O. longinoda* colonies (see above and Fig. 4) shows that these caterpillars were able to appease the ants despite lacking the Newcomer gland (Pierce et al. 2002).

Lycaenid caterpillars living on plants

That all of the lycaenid species studied whose caterpillars develop entirely on the host plant foliage are associated with one or a small number of ant species is likely related to ant-dependent oviposition (i.e., adult lepidopteran females laying their eggs using ant cues) (see Kaminski et al. 2010 and Bächtold et al. 2014 for florivorous caterpillars). For example, the presence of the weaver ant *O. smaragdina* is detrimental to female oviposition for the polyommatine *Anthene emolus* (Fiedler and Maschwitz 1989).

The nutritional rewards secreted by the Newcomer gland, repeatedly noted in this study for two Theclinae species, ensure ant presence and so constant protection for the caterpillars that can also mediate the amount of protection they receive by modifying the quantity of compounds produced (Pierce et al. 2002). Yet, the presence of this gland is not necessary to maintain an efficacious association with ants. For example, *Lycaena xanthoides* (Lycaeninae) caterpillars, which do not possess a Newcomer gland, attract ants when they are perturbed, likely through the action of their pore copula organs (Oliver and Stein 2011). The appeasing role of pore copula
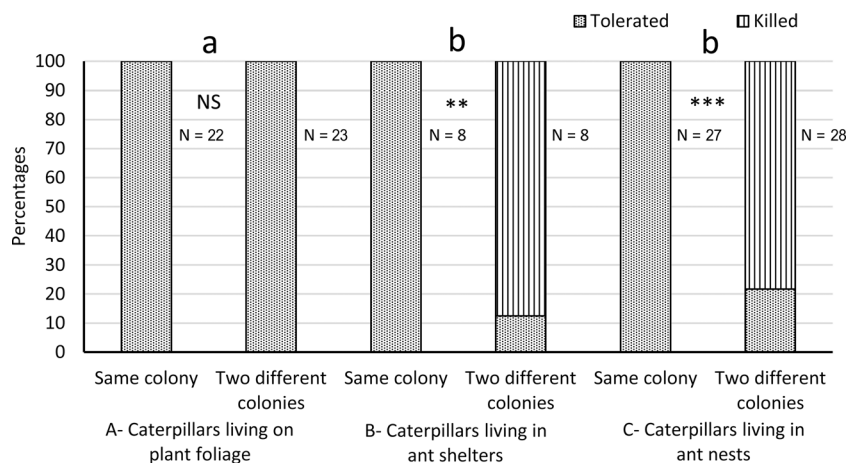

Fig. 4 Reactions (tolerate or kill) of ant workers toward caterpillars which were transferred from one part of the host plant to a place occupied by workers from the same colony several meters away versus when the caterpillars were transferred from one plant to another sheltering a neighboring, alien colony of the same ant species. *A* Lycaenid caterpillars (Theclinae) that are defoliators and/or nectarivorous living on plant foliage (*Aphneus orcas* on *Crematogaster striatula* territories; *Dapidodigma demeter* on *Oecophylla longinoda* territories); *B* lycaenid caterpillars that feed on ant-attended hemipterans in shelters (*Lachnocnema emperamus* in *Camponotus brutus* shelters); and *C* lycaenid and noctuid caterpillars which live inside *O. longinoda* nests

(*Euliphyra leucyania*; *Eublemma albifascia*). Statistical comparisons for each situation, Fisher's exact test for count data (*NS* non-significant, *P < 0.05, **P < 0.01, ***P < 0.001). Comparison between situations (Fisher's exact test and BH correction) for both caterpillar and ant transfers: *different letters* indicate a significant difference at *P* < 0.01. Ant workers transferred between two distant areas of one territory were always accepted (similarity between caterpillars and ants), while those transferred to the territory of another conspecific colony were always killed. This results in a significant difference (1) with the caterpillars living on the host plant foliage that were always accepted and (2) with the caterpillars living in ant nests for which 21.42 % survived the transfer

organs on nearby ants was also shown for the first two instar caterpillars of *Ogyris amarilis* (Theclinae), the Newcomer gland appearing on later instars (Atsttat 1981).

Lycaenid caterpillars living as parasites in ant nests

Here, too, ant-dependent oviposition was noted in this study for *Euliphyra*, a situation identical to that of the noctuid *E. albifascia* (Dejean et al. 2016). Similarly, *L. brassolis* females (Melitinae) oviposit on the foliage of trees sheltering *O. smaragdina* nests (Pierce et al. 2002) and *Anthene usamba* (Polyommatinae) females lay their eggs on the foliage of myrmecophytic acacia sheltering a *Crematogaster mimosae* colony (Martins et al. 2013).

Because both *Euliphyra* spp. and *E. albifascia* caterpillars are constantly licked by *O. longinoda* workers, we suggest that, in addition to the role of CHCs in their chemical camouflage, attractive secretions facilitate their integration into the colonies (i.e., pore copula organs for *Euliphyra*; the equivalent for *E. albifascia*). Yet, it has been shown that *L. brassolis* caterpillars possess pore copula organs that play a major role in their acceptance in *O. smaragdina* nests as their CHCs do not match those of their host ants (Dupont et al. 2016).

In conclusion, this study illustrates that the caterpillars living on plant foliage in the presence of TDAAs are protected by silk (defoliators), use mostly biosynthesized chemicals to lower ant aggressiveness (defoliator and/or nectarivorous, lichen or ant-attended feeders), or have long bristles (lichen feeders). Other caterpillars live in ant shelters or ant nests where they likely acquire the host colony odor; they are brood feeders or cuckoo parasites. This study also contributes to explain how *Alchornea*, which develops naturally along rivers and has spread along forest edges, tracks and open areas, favor the presence of numerous insects in spite of the anthropogenic disturbance to the environment. This is the case for TDAAs and insects adapted to their presence (this study) plus non-territorial ants and the cohort of associated or tolerated insects (AD, pers. obs.). This plant species has therefore a major conservation value, particularly when it presence interconnects forest remnants in a fragmented landscape.

References

Akino T (2008) Chemical strategies to deal with ants: a review of mimicry, camouflage, propaganda and phytomimesis by ants (Hymenoptera: Formicidae) and other arthropods. Myrmecol News 11:173–181

Atsatt PR (1981) Lycaenid butterflies and ants: selection for enemy-free space. Amer Nat 118:638–654

Bampton I (1995) A discussion on the larval food of the subfamily Lipteninae (Lepidoptera, Lycaenidae). Metamorphosis 6:62–166

Bächtold A, Alves-Silva E, Kaminski LA, Del-Claro K (2014) The role of tending ants in host plant selection and egg parasitism of two facultative myrmecophilous butterflies. Naturwissenschaften 101: 913–919

Bouyer T (1997) Contribution à la révision du genre *Hewitsonia* avec description d'une sous-espèce et de 4 espèces nouvelles. Études sur les Lycaenidae: no. 4. (Lepidoptera, Lycaenidae). Lambillionea 97: 82–98

Boyle JH, Kaliszewska ZA, Espeland M, Suderman TR, Fleming J, Heath A, Pierce NE (2015) Phylogeny of the Aphnaeinae: myrmecophilous African butterflies with carnivorous and herbivorous life histories. Syst Entomol 40:169–182

Callaghan CJ (1992) Biology of epiphyll feeding butterflies in a Nigerian cola forest (Lycaenidae: Lipteninae). J Lepidopt Soc 46:203–214

Callaghan CJ (1993) Notes on the biology of a myrmecophilous African lycaenid, *Aphnaeus adamsi* Stempffer (Lepidoptera, Lycaenidae). Bull Soc Entomol Fr 97:339–342

Clark GC, Dickson CGC (1971) Life histories of the South African lycaenid butterflies. Purnell and Sons, Cape Town

Collet J-Y (1996) The tree and the ants. Video movie 50′; The Discovery Channel http://www.jeanyvescollet.com/les-films-extraits-dossiers/95-films/extraits-flash/145-l-arbre-et-les-fourmis

Collet J-Y (2004) Secrets of the African jungle—ants. Video movie 50′, The Discovery Channel; http://www.vodeo.tv/documentaire/les-fourmis#play

Cripps C, Jackson THE (1940) The life history of *Lachnocnema bibulus* (fab.) in Kenya (Lepidopt., Lycaenidae), with a note on the larval gland by Dr H. Eltringham, FRS. Trans R Entomol Soc London 90: 449–453

d'Ettorre P, Lenoir A (2010) Nestmate recognition. In: Lach L, Parr CL, Abbott KL (eds) Ant ecology. Oxford University Press, Oxford, pp 194–209

Daniels H, Gottsberger G, Fiedler K (2005) Nutrient composition of larval nectar secretions from three species of myrmecophilous butterflies. J Chem Ecol 31:2805–2821

Dejean A, Azémar F, Roux O (2014) An invasive ant species counterattacks marabunta raids. C R Biol 337:474–479

Dejean A, Beugnon G (1996) Host-ant trail following by myrmecophilous larvae of Liphyrinae (Lepidoptera, Lycaenidae). Oecologia 106:57–62

Dejean A, Corbara B (2014) Reactions by army ant workers to nestmates having had contact with sympatric ant species. C R Biol 337:642–645

Dejean A, Corbara B, Orivel J, Leponce M (2007) Rainforest canopy ants: the implications of territoriality and predatory behavior. Funct Ecosyst Commun 1:105–120

Dejean A, Gibernau M (2000) A rainforest ant mosaic: the edge effect. Sociobiology 35:385–401

Dejean A, Orivel J, Azémar F, Hérault B, Corbara B (2016) A cuckoo-like parasitic moth leads African weaver ant colonies to their ruin. Sci Rep 6:23778

Dejean A, Ryder S, Bolton B, Compin A, Leponce M, Azémar F, Céréghino R, Orivel J, Corbara B (2015) How territoriality and host-tree taxa determine the structure of ant mosaics. Sci Nat 102:33

DeVries PJ (1991) Foam barriers, a new defense against ants for milkweed butterfly caterpillars (Nymphalidae: Danainae). J Res Lepidopt 30:261–266

Dodd FP (1912) Some remarkable ant-friend Lepidoptera. Trans Entomol Soc London 1911:577–590

Dupont ST, Zemeitat DS, Lohman DJ, Pierce NE (2016) The setae of parasitic *Liphyra brassolis* butterfly larvae form a flexible armour for resisting attack by their ant hosts (Lycaenidae: Lepidoptera). Biol J Linn Soc 117:607–619

Farquharson CO (1921) Five years' observation (1914-1918) on the bionomics of southern Nigerian insects, chiefly directed to the investigation of lycaenid life-histories and to the relation of Lycaenidae, Diptera, and other insects to ants. Trans Entomol Soc London 1921: 319–448

Fiedler K (1991) Systematic, evolutionary, and ecological implications of myrmecophily within the Lycaenidae (Insecta: Lepidoptera: Papilionoidea). Bonner Zool Monogr 31:1–210

Fiedler K (1994) Lycaenid butterflies and plants: is myrmecophily associated with amplified host-plant diversity? Ecol Entomol 19:79–82

Fiedler K (2012) The host genera of ant-parasitic Lycaenidae butterflies: a review. Psyche:ID 153975

Fiedler K, Maschwitz U (1989) The symbiosis between the weaver ant, *Oecophylla smaragdina*, and *Anthene emolus*, an obligate myrmecophilous lycaenid butterfly. J Nat Hist 23:833–846

Fitzgerald TD (1996) The tent caterpillars. Cornell University Press, Ithaca, NY

Foottit RG, Adler PH (2009) Insect biodiversity, John Wiley & Sons, New York

Forister ML, Gompert Z, Nice CC, Forister GW, Fordyce JA (2011) Ant association facilitates the evolution of diet breadth in a lycaenid butterfly. Proc R Soc B 278:1539–1547

Herbison-Evans D, Crossley SA (2016) Cardamyla carinentalis Walker, 1859 (Pyralini, Pyralinae, Pyralidae, Pyraloidea). http://lepidoptera.butterflyhouse.com.au/pyra/carinen.html

Jackson THE (1947) The early stages of some African Lycaenidae (Lepidoptera: Rhopalocera). Proc R Entomol Soc London A 22: 44–48

Kaliszewska ZA, Lohman DJ, Sommer K, Adelson G, Rand DB, Mathew J, Talavera G, Pierce NE (2015) When caterpillars attack: biogeography and life history evolution of the Miletinae (Lepidoptera: Lycaenidae). Evolution 69:571–588

Kaminski LA, Freitas AVL, Oliveira PS (2010) Interaction between mutualisms: ant-tended butterflies exploit enemy-free space provided by ant-treehopper associations. Amer Nat 176:322–334

Kemner NA (1923) Hyphaenosymphilie, eine neue merkwürdige art von myrmekophilie bei einem neuen myrmeckophilen schmetterling (*Wurthia aurivillii* n. sp.) aus Java beobachtet. Arkiv Zool 15:1–28

Lamborn WA (1914) On the relationship between certain west African insects, especially ants, Lycaenidae and Homoptera. Trans Entomol Soc London 1913:436–498

Leclerc J-B, Detrain C (2016) Ants detect but do not discriminate diseased workers within their nest. Sci Nat 103:70

Lenoir A, D'Ettorre P, Errard C, Hefetz A (2001) Chemical ecology and social parasitism in ants. Annu Rev Entomol 46:573–599

Libert M (1999) Révision des *Epitola* (l. s.) - Révision des genres *Epitola* Westwood, *Hypophytala* Clench et *Stempfferia* Jackson, et description de trois nouveaux genres (Lepidoptera, Lycaenidae). ABRI-Lambillionea 1–227

Libert M (2010) Révision des *Anthene* africains (Lepidoptera, Lycaenidae). ABRI-Lambillionea:1–420

Libert M (2016) African Liphyrini: updating the taxonomy (Lepidoptera, Lycaenidae). ABRI- Libert M Ed., MJBSAS-Librairie Top Duck, Amboise, p 1–129

Martins DJ, Collins SC, Congdon C, Pierce NE (2013) Association between the African lycaenid, *Anthene usamba*, and an obligate acacia ant, *Crematogaster mimosae*. Biol J Linn Soc 109:302–312

Mavar-Manga H, Lejoly J, Quetin-Leclercq J, Schmelzer GH (2007) Alchornea cordifolia (Schumach. & Thonn.) Müll.Arg. In: Schmelzer, GH, Gurib-Fakim A (Editors), Plant Resources of Tropical Africa, Wageningen, The Netherlands, http://www.prota4u.org/search.asp

Moss JT (1989) Observations of *Hypolycaena phorbas phorbas* (Fabricius) (Lepidoptera: Lycaenidae) on Carlisle Island, Queensland. Aust Entomol Mag 16:85–86

Oliver JC, Stein LR (2011) Evolution of influence: signaling in a lycaenid-ant interaction. Evol Ecol 25:1205–1216

Parsons MJ (1999) The butterflies of Papua New Guinea: their systematics and biology. Academic Press, London

Panis A (1974) Action prédatrice d'*Eublemma scitula* (Lepidoptera Noctuidae, Erastriinae) dans le sud de la France. Entomophaga 19: 493–500

Passera L, Aron S (2005) Les fourmis: comportement, organisation sociale et évolution. Les Presses scientifiques du CNRC, Ottawa

Pierce NE (1995) Predatory and parasitic Lepidoptera: carnivores living on plants. J Lepidopt Soc 49:412–453

Pierce NE, Braby MF, Heath A, Lohman DJ, Mathew J, Rand DA, Travassos MA (2002) The ecology and evolution of ant association in the Lycaenidae (Lepidoptera). Annu Rev Entomol 47:733–771

Pike N (2011) Using false discovery rates for multiple comparisons in ecology and evolution. Met Ecol Evol 2:278–282

Regier JC, Mitter C, Solis M, Hayden J, Landry B, Nuss M, Simonsen T, Yen S, Zwick A, Cummings M (2012) A molecular phylogeny for the pyraloid moths (Lepidoptera: Pyraloidea) and its implications for higher-level classification. Syst Entomol 37:635–656

Rifflet A, Tene N, Orivel J, Treilhou M, Dejean A, Vetillard A (2011) Paralyzing action from a distance in an arboreal African ant species. PLoS One 6:e28571

Robinson CS, Tuck KR, Shaffer M (1994) A field guide to the smaller moths of South-East Asia. Malaysia Nature Society, Art Printing Works, Kuala Lumpur, Malaysia

Roepke W (1916) Eine neue myrmekophile Lepidoptere aus Java (*Wurthia myrmecophila* n. g., n. sp.). Zoolog Mededeel 2:141–146

Roessingh P (1990) Chemical trail marker from silk of *Yponomeuta cagnagellus*. J Chem Ecol 16:2203–2216

Rosta M, Blassmann K (2009) Insects had it first: surfactants as a defence against predators. Proc R Soc London, B 276:633–638

Roux O, Céréghino R, Solano PJ, Dejean A (2011) Caterpillars and fungal pathogens: two co-occurring parasites of an ant-plant mutualism. PLoS One 6:e20538

Roux O, Martin J-M, Tene Ghomsi N, Dejean A (2009) Non-lethal water-based removal-reapplication technique for the cuticular compounds of ants. J Chem Ecol 35:904–912

Roux O, Rossi V, Céréghino R, Compin A, Martin J-M, Dejean A (2013) How to coexist with fire ants: the roles of behaviour and cuticular compounds. Behav Proc 98:51–57

Samson C, Smart P (1980) A review of the genus *Liphyra* (Lepidoptera: Lycaenidae) of Indo-Australia, with descriptions of two new subspecies from the Solomon archipelago. The Aurelian 1:6–16

Seth-Smith DW (1938) Life histories of some butterflies in the northern territories, gold coast (Lepid.). Proc R Entomol Soc London A 13: 141–154

Smedley SR, Schroeder FC, Weibel DB, Meinwald J, Lafleur KA, Renwick JA, Rutowski R, Eisner T (2002) Mayolenes: labile defensive lipids from the glandular hairs of a caterpillar (*Pieris rapae*). Proc Natl Acad Sci U S A 99:6822–6827

Solis MA, Maes KVN (2002) Preliminary phylogenetic analysis of the subfamilies of Crambidae (Pyraloidea Lepidoptera). Belg J Entomol 4:53–95

Tokeshi M, Yoko-O M, Daud JRP, Domits M (2007) *Hypolycaena erylus* feeding on mangrove apple and attended by *Oecophylla* weaver ants, in North Sulawesi, Indonesia (Lepidoptera: Lycaenidae). Trop Lepidopt 17:35–36

Tschinkel WR (2011) Back to basics: sociometry and sociogenesis of ant societies (hymenoptera: Formicidae). Myrmecol News 14:49–54

Van Wilgenburg E, Symonds MRE, Elgar MA (2011) Evolution of cuticular hydrocarbon diversity in ants. J Evol Biol 24:1188–1198

Vu NT, Eastwood R, Nguyen CT, Pham LV (2006) The fig wax scale *Ceroplastes rusci* (Linnaeus) (Homoptera: Coccidae) in south-east Vietnam: pest status, life history and biological trials with *Eublemma amabilis* Moore (Lepidoptera: Noctuidae). Entomol Res 36:196–201

Williams MC (2008-2016) Butterflies and skippers of the Afrotropical region (Papilionoidea and Hesperioidea). File L – Aphnaeini (Lycaenidae). File M – Lycaeninae, Polyommatinae (Lycaenidae). File N – Miletinae (Lycaenidae). http://atbutterflies.com/index.htm

Young AM (1986) Natural history notes on *Brassolis isthmia* bates Lepidoptera: Nymphalidae: Brassolinae in northeastern Costa Rica. J Res Lepidopt 24:385–392