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The influence of ants on patterns of colonization and establishment within a set of coexisting lycaenid butterflies in a south-east Asian tropical rain forest

Abstract In Peninsular Malaysia ten species of lycaenid butterflies use leaf flushes or inflorescences of the legume tree *Saraca thaipingensis* as larval hostplant. Resource partitioning among these species is regulated by a complex mixture of patterns of interaction with ants. Females of obligately myrmecophilous species lay their eggs exclusively on trees colonized by their specific host ants. On trees colonized by weaver ants, only specialist mutualists adapted to these territorial ants are able to survive, while larvae of other species are killed. The formicine ant *Cladomyrma petalae*, which inhabits hollow twigs of the myrmecophytic hostplant, likewise precludes oviposition by female butterflies. Lycaenid larvae confronted with this ant species never survive, but one concealed feeding species (*Jamides caeruleus*) escapes removal due to the cryptic life-habits of the larvae. Two facultative myrmecophiles associate in a mutualistic way with a wide and largely overlapping range of ant genera which forage at the extrafloral nectaries of leaf flushes. One species (*Cheritra freja*) is not myrmecophilous, but is tolerated by all but the most territorial ants. Ant-dependent hostplant selection and egg-clustering characterize the obligate mutualists, whereas facultative myrmecophiles and the non-myrmecophile distribute their eggs singly over appropriate hostplants. Signals mediating caterpillar-ant communication are highly specialized in one obligate myrmecophile (*Drupadia theda*), but rather unspecific in four other species tested. Altogether our observations indicate that colonization and establishment of lycaenid butterflies on *S. thaipingensis* trees are governed by specializations as well as opportunistic use of resources (ants and hostplant parts). Therefore, the diversity of this species assemblage is maintained by deterministic as well as stochastic factors.

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Introduction

Ants may act on butterflies in multiple ways. In most terrestrial habitats, ants are among the leading arthropod predators (Hölldobler and Wilson 1990) and they potentially prey on all stages of a butterfly's life cycle from the egg to the adult. Many plants use this predacious capacity of ants to obtain protection from herbivores like butterfly larvae. An enormous diversity of plants attract ants with the help of food bodies or nutritious secretions from extrafloral nectaries (EFN hereafter) (Koptur 1992; Fiala and Linsenmair 1995). Moreover, true myrmecophytes provide nesting space for ants, often in addition to food rewards (e.g. Benson 1985). Evidence of protection from herbivory through ant guards is abundant, although not universal, for myrmecophytes as well as EFN plants (Janzen 1966; Beattie 1985; Huxley and Cutler 1991). Ants may protect ant-attracting plants from butterfly herbivory in two ways. Either they remove the butterflies' immature stages while foraging on these plants, or they drive away adult females in search for oviposition sites, thus preventing butterfly colonization.

Larvae of the butterfly family Lycaenidae provide a particular case. To evade antagonistic influences of ants on their hostplants, lycaenid larvae have evolved mechanisms which appease these aggressive hymenopterans. Quite a number of lycaenid larvae even form stable associations with ants. Appeasement as well as permanent associations are mainly mediated by the secretions of specialized larval and pupal glands (Cottrell 1984; Fiedler 1991). Although information on the chemical composition of their secretions is still fragmentary, it is evident from behavioural observations that the secretions are particularly attractive to ants. The dorsal nectar organ plays a key role in butterfly-ant interactions. Myrmecophilous larvae deliver liquid droplets containing carbohy-

drates and amino acids from this gland (Maschwitz et al. 1975; Pierce 1983; Cushman et al. 1994; Wagner 1994) and thereby induce food recruitment and continuous tending behaviour in ants (Fiedler and Maschwitz 1989a).

Food rewards from the dorsal nectar organ of lycaenid larvae can contribute substantially to the nourishment or even growth of an ant colony (Pierce et al. 1987; Fiedler and Maschwitz 1988; Nash 1989; Fiedler and Saam 1995). The butterfly larvae, in turn, benefit from continuous tending in terms of protection against parasitoids or predators (e.g. Pierce and Easteal 1986; Pierce et al. 1987) or enhanced development (Fiedler and Hölldobler 1992; Wagner 1993; Cushman et al. 1994). Therefore, appeasing ants does not only allow peaceful coexistence, but may also result in mutualistic symbioses between lycaenids and ants with benefits accruing to both partners. Such mutualistic relationships range from facultative and unspecific, to obligatory and host-specific associations. Obligately myrmecophilous lycaenids even select their hostplants using ants as oviposition cues (Atsatt 1981; Pierce and Elgar 1985).

In a number of lycaenid butterflies, however, the larvae do not have a nectar gland and, accordingly, interactions with ants are restricted to the level of coexistence through mere appeasement (Fiedler 1991). Such species are termed myrmecoxenes hereafter. Finally, appeasing of ants may on occasion fail so that lycaenid larvae also suffer from ant predation (Samson and O'Brian 1981).

Hence, ants may behave towards lycaenid immatures as mutualistic partners or as predators, they may serve to attract egg-laying females, or they may behave neutrally towards myrmecoxenous caterpillars. Due to this diversity of relationships between lycaenid butterflies and ants, these hymenopterans are an important component within the multidimensional ecospace faced by the members of any set of lycaenid species. Interactions with ants may amplify lycaenid diversity (Pierce 1984), because they provide another dimension for ecological segregation, additional to traits such as hostplant use, phenology, voltinism, habitat partitioning, adult resource partitioning, and other types of parasite and predator escape (Gilbert and Singer 1975; Vane-Wright 1978). In humid tropical

forests with their extremely high species diversity of lycaenid butterflies as well as ants, this diversity-enhancing role of myrmecophilous interactions could be expected to be particularly pronounced. We therefore set out to study the various effects that ants may potentially have on the species structure and diversity of, and resource partitioning among, lycaenid butterflies. We were also interested in the interference between mutualistic ant-plant associations and the outcome of butterfly-ant interactions.

For our investigations we chose the assemblage of lycaenid species whose larvae feed on the south-east Asian legume tree Saraca thaipingensis (Caesalpiniaceae). S. thaipingensis is abundant and easily accessible at riversides on the Malay Peninsula. Leaf flushes and inflorescences of S. thaipingensis are utilized as larval food by at least ten lycaenid species. Young leaves bear extrafloral nectaries which attract ants from various genera (Fiala et al. 1994; P. Seufert and K. Fiedler, personal observation). In addition, S. thaipingensis is a facultative myrmecophyte whose hollow twigs are often colonized by ants, in particular by the specialized formicine ant Cladomyrma petalae (Maschwitz et al. 1991). Collectively, these features render S. thaipingensis a promising target for ecological and behavioural studies of complex interactions between butterflies, ants, and plants.

Material and methods

Study site

Our study was conducted along the banks of the Gombak river and its tributaries, located in the Gombak valley (3°21' N, 101°42' E) at the foothills of the Genting Highlands about 20 km north of the Malaysian capital Kuala Lumpur (Peninsular Malaysia). The area (200–400 m a.s.l.) is predominatly covered with advanced secondary forest of the lowland dipterocarp type (Whitmore 1988), with partial disturbance through small plantations of local people. Details on the vegetation can be found in Medway (1972). Observations and experiments were made in 1988 and in the years 1991–1995. The legume tree Saraca thaipingensis (Caesalpiniaceae) is one of the most characteristic riverside trees of Peninsular Malaysia, giving rise to the term "Saraca streams" for mountain rivers like the Sungai Gombak (Corner 1988). Trees grow up to 15 m height, but due to occasional coppicing by native people and

Table 1 Hostplant use and myrmecophily among the 10 lycaenid species whose larvae feed on Saraca thaipingensis

Lycaenid species	Lycaeninae tribe	Hostplant range (number of plant families used)	Degree of myrmecophily	Naturally tended by
Semanga superba	Theclini	Oligophagous (2)	Obligate myrmecophile	Dolichoderus sp.
Cheritra freja	Eumaeini	Polyphagous (7)	Myrmecoxene	Untended
Drupadia ravindra	Eumaeini	Polyphagous (6)	Facultative myrmecophile	Various ant genera
Drupadia theda	Eumaeini	Polyphagous (6)	Obligate myrmecophile	Crematogaster sp.
Hypolycaena erylus	Eumaeini	Polyphagous (4)	Obligate myrmecophile	Oecophylla smaragdina
Rapala pheretima	Eumaeini	Polyphagous (7)	Obligate myrmecophile	Oecophylla smaragdina
Anthene emolus	Polyommatini	Polyphagous (6)	Obligate myrmecophile	Oecophylla smaragdina
Jamides pura	Polyommatini	Oligophagous (2)	Facultative myrmecophile	Various ant genera
Jamides caeruleus	Polyommatini	Monophagous	Facultative myrmecophile	Mostly untended
Jamides celeno	Polyommatini	Polyphagous (4)	Facultative myrmecophile	Various ant genera

the natural tendency of *S. thaipingensis* to produce young adventive sprouts, accessible leaf flushes (0.5–4 m above ground) were available in fluctuating numbers year-round. The conspicuous yellow inflorescences emerge from the stems or thicker branches (cauliflory), main flowering season is in January and February. Young leaves and inflorescences are heavily attacked by a variety of herbivores, including moth larvae, chrysomelid beetles and katydids.

Lycaenids on *Saraca thaipingensis*

Ten lycaenid species, all in the subfamily Lycaeninae, are known to feed on *Saraca thaipingensis*. Except for *Jamides celeno* (see Eliot 1992), we found the larvae of all these species on *Saraca thaipingensis* in the Gombak valley. Most of them do not exclusively use *Saraca thaipingensis* as larval host (see Table 1). The life history of *Semanga superba* had previously been unknown (Fiedler and Seufert 1995). Partial accounts on larval and pupal morphology, hostplant use, and ant associations of most of the remaining study species were given by Eliot (1992), Fiedler and Maschwitz (1989b) and Maschwitz et al. (1985). Starting from this background, we discovered a multitude of new aspects concerning hostplant ranges, relationships with ants, and larval and adult behaviour of these lycaenids.

While eggs and larvae of six species (*Cheritra freja, Drupadia ravindra, D. theda, Anthene emolus, Jamides pura, J. caeruleus*) were relatively abundant on *Saraca thaipingensis* during our investigations, immature stages of the other species were rare. Therefore, conclusions on specializations, resource partitioning, and mechanisms of coexistence are mainly based on observations made on, and experiments conducted with, the six more abundant species.

Methods

A great proportion of the data on female oviposition behaviour, hostplant use, larval behaviours and ant associations were sampled during unmanipulated field observations. We routinely inspected all available leaf flushes or inflorescences of *Saraca thaipingensis* during transect walks along the river banks to observe the behaviours of butterflies and their immature stages. Some behavioural observations made on hostplants other than *S. thaipingensis* during the transect walkes are added. Specifically, we recorded the following aspects during these transects:

1. Oviposition behaviour, the number of eggs laid during oviposition acts, and the presence of ants and their behaviour towards the butterflies during oviposition
2. Size of egg-batches of each species, and the presence and identity, or absence of, ants on the plant parts carrying the eggs
3. Presence, number and age of lycaenid larvae, exact locality of feeding, and the absence/presence/identity of ants on the plant part colonized
4. Larval behaviours and, if present, the type and intensity of caterpillar-ant interactions under natural conditions.

In lycaenid species with an obligate relationship towards a specific ant species or genus, female butterflies often show ant-dependent oviposition behaviour (Pierce and Elgar 1985). Especially in tropical rain forests with their highly diverse ant fauna, where ecologically dominant ant species are patchily distributed, females of obligate myrmecophiles can be expected to effectively recognize proper host ants. Females should also avoid fatal attacks by aggressive ants during their search for oviposition sites, either by appeasing ants during egg-laying or by fast escape reactions. Facultative myrmecophiles or myrmecoxenes, in contrast, might not use particular ant species as oviposition cues, and the presence of a suitable part of a hostplant alone should be sufficient to induce egg-laying. Hence, observations on oviposition behaviour and recording the presence and identity of ants at egg batches yield important information as to the specificity and obligateness of a butterfly's ant-association. To assess experimentally the significance

of ants for oviposition and larval survival, we applied sticky barriers of Tanglefoot on selected young leaf flushes of *S. thaipingensis*, which were inaccessible to ants after this treatment.

We also experimentally investigated the specificity of communication signals mediating caterpillar-ant associations. Eggs and young larvae were collected in the field and reared in the laboratory in transparent plastic boxes (250 ml) with ad libitum food under ambient temperatures, until they reached the final (= fourth) instar. For laboratory experiments, we confined individual final instar larvae with samples of 1–15 workers of the same ant species, depending on the ants' size. These trials were run in translucent plastic vials (125 or 250 ml) lined with filter paper. Each caterpillar was tested only once a day. The experiments lasted 15–30 min. The ants chosen for experiments represented species which commonly forage *S. thaipingensis* trees at the study sites. In addition to the laboratory experiments, we placed single mature larvae on leaf flushes of *S. thaipingensis* trees which were inhabited, or foraged on, by particular ant species. Subsequently, we observed the outcome of such encounters for at least 2 h.

During experimental encounters in the field or laboratory, we recorded how the ants behaved towards the test caterpillars, whether the larvae were able to establish stable associations with ants, and whether secretions were delivered from the dorsal nectar organ. The mean number of ants in direct contact with a caterpillar, censused every 30 s over 15 min test intervals, served as a measure of "attractiveness" of mature larvae towards ants. This was only measured in caterpillar-ant associations which had been established for at least 1 h. The data on attractiveness were statistically evaluated using one-way ANOVA separately for each ant genus, followed by multiple comparisons after Scheffé's method (Sachs 1992). To obtain normality and equalize variances, we transformed the values of attractiveness by log (attractiveness + 3/8). Butterflies were identified after Eliot (1992). Ant samples were identified to genus level (Bolton 1994). Vouchers of ants and butterflies are housed in the authors' collections.

Results

Natural associations between lycaenid larvae and ants

All combinations of ants with larvae of nine lycaenid species, which we have so far found on *S. thaipingensis* in the field around Ulu Gombak, are summarized in Table 2. In this table and throughout this paper, "stable association" means that a larva was almost continuously tended by one or more worker ants, which showed no signs of aggressiveness. Typically, the ants intensively antennated the caterpillar and imbibed secretion droplets from its nectar organ. Brief encounters (< 10 s) between a caterpillar and ants, implying only a short antennal inspection, are not regarded as stable ant-association, but indicate that ants tolerate larvae due to some effective appeasement mechanism (e.g. with myrmecoxenous larvae).

In *Drupadia ravindra* and *Jamides pura* associations with ants are facultative, and there is no specific relationship to particular visiting ants. Ranges of ant partners are similar in both species and represent most of the ant taxa commonly found to forage on *S. thaipingensis* at the Gombak riverside. Although older larvae possess a full complement of functional ant organs, 6.2 or 19.2%, respectively, of the individuals were not associated with ants at the time of observation.

Jamides caeruleus can also be considered to be a facultative and unspecific myrmecophile, but 96.6% of the

Table 2 Stable associations between ants and larvae of nine lycaenid species in the Gombak valley (given are numbers of observed larvae). Only third and fourth instar larvae are considered, because younger instars of the facultatively myrmecophilous lycaenids do not yet have a functional nectar organ and are thus normally not tended by ants. Ant subfamilies are abbreviated in parentheses (*Myr* Myrmicinae, *Dol* Dolichoderinae, *For* Formicinae)

Ant genus (subfamily)	Lycaenid-species								
	Semanga superba	*Drupadia theda*	*Hypolycaena erylus*	*Rapala pheretima*	*Anthene emolus*	*Drupadia ravindra*	*Jamides pura*	*Jamides caeruleus*	*Cheritra freja*
Crematogaster (Myr)		187				1	5		
Tetramorium (Myr)						6			
Rhoptromyrmex (Myr)						1	2		
Meranoplus (Myr)							5		
Myrmicaria (Myr)						1			
Acanthomyrmex (Myr)						2	3		
Pheidole (Myr)						1			
Dolichoderus (Dol)	3								
Technomyrmex (Dol)						5	9		
Tapinoma (Dol)						3	6	3	
Oecophylla (For)			7	11	>200				
Paratrechina (For)						1			
Found without tending ants						5	2	86	38
Percentage of larvae tended by ants	100	100	100	100	100	80.8	93.8	3.4	0

larvae were found without tending ants. This low incidence of ant-association is due to the hidden life-habit of *J. caeruleus* larvae, which rest and feed inside flower buds or in shelters made from petals spun together with silk, where they are inaccessible to all but the smallest ants (e.g. one tiny *Tapinoma* species).

Larvae of *Cheritra freja* are myrmecoxenous. They lack a dorsal nectar organ and tentacle organs and were never found in stable associations with ants in the field. During casual encounters with ants of the genera *Crematogaster, Tapinoma, Technomyrmex, Camponotus*, and *Polyrhachis*, which foraged on leaves inhabited by *Cheritra freja* caterpillars, these ants at most briefly antennated the larvae and left them unharmed after a few seconds. If a larva was feeding during an encounter, however, ants often stayed near the feeding damage caused by the caterpillar and imbibed the plant sap issuing out.

The remaining five butterfly species have been observed in association exclusively with ants from one species or genus. *Anthene emolus* and *Hypolycaena erylus* specifically live in association with the extremely aggressive weaver ant *Oecophylla smaragdina* (Fiedler and Maschwitz 1989b; Eliot 1992). A third species associated with *O. smaragdina* is *Rapala pheretima*. Young larvae of this species were occasionally (*n* = 3) found without tending ants, especially when highly attractive *A. emolus* caterpillars lived on the same hostplant. Yet there is little doubt that *R. pheretima* is a specific myrmecophile, because even the untended larvae lived in close proximity to nests or trails of *O. smaragdina*. Specificity of *R. pheretima* to weaver ants is also indicated by oviposition behaviour (see below).

Drupadia theda is obligatorily and specifically associated with two *Crematogaster* species, as indicated by the high number of larvae found in association with only these ants in the field, female oviposition behaviour (see below), specificity of larval communication signals (see below) and strong reduction of larval survival without tending ants (P. Seufert and K. Fiedler, to be published). The very close and persistent association of *Semanga superba* larvae with *Dolichoderus* ants may also indicate an obligate and specific relationship (Fiedler and Seufert 1995).

Oviposition behaviour in relation to presence of ants

The outcome of interactions between egg-laying female lycaenid butterflies and ants foraging on the presumptive larval hostplant are summarized in Table 3. As expected, we observed egg-laying in the four obligate myrmecophiles *Drupadia theda, Hypolycaena erylus, Rapala pheretima*, and *Anthene emolus* exclusively on plants inhabited by their specific ant partners. Non-aggressive contacts between *Crematogaster* workers and egg-laying *D. theda* females occurred in 50% of all observed oviposition acts (*n* = 10). At *S. thaipingensis* trees inhabited by *Crematogaster* ants, *D. theda* females repeatedly (*n* = 8) approached young leaf flushes which had previously been used for oviposition, but later had been rendered ant-free by means of sticky barriers. The butterflies still closely investigated the ant-free leaf flushes with their antennae and the tip of the abdomen, but never started to lay eggs. On unmanipulated twigs foraged by *Crematogaster* ants, *D. theda* females laid eggs for up to 14 days, as long as leaf flushes remained in suitable condition.

Oecophylla smaragdina workers always reacted aggressively towards female butterflies approaching them during their examination flights. Such attacks caused the facultative myrmecophile *Drupadia ravindra* or the my-

Table 3 Oviposition behaviour of female lycaenid butterflies in relation to the presence of ants, and the reactions of ants towards egg-laying butterflies. "Artificially ant-free" refers to young leaf flushes of *Saraca thaipingensis* trees which were rendered inaccessible to ants by application of sticky barriers [0 no oviposition, female deterred by aggressive ants, *1* oviposition on plants without ants (*a* artificially ant-free, *b* naturally ant-free, *c* in flight cage without ants), *2* oviposition on plants with ants, but no contact between butterfly and ants, *3* oviposition on plants with ants, non-aggressive contact, *4* oviposition on plants with ants, after initial aggressive behaviour of ants (*a* egg-laying without contact between butterfly and ants, *b* egg-laying with non-aggressive contact)]

Ants on hostplant	Lycaenid species							
	Drupadia theda	*Hypolycaena erylus*	*Rapala pheretima*	*Anthene emolus*	*Drupadia ravindra*	*Jamides pura*	*Jamides caeruleus*	*Cheritra freja*
Crematogaster	2,3				2	2		2
Technomyrmex					2,3	2		2
Tapinoma					2		2	
Oecophylla		4a	4a	4b	0			0
Camponotus								2
Cladomyrma							2	
Artificially or naturally ant free					1a,b	1c	1b	1a,b

Table 4 Egg-clutch sizes and total numbers of eggs laid by females of eight lycaenid species in the Gombak valley

Clutch size (number of eggs)	Lycaenid species Cumulative number of eggs deposited in respective clutch size							
	Anthene emolus	*Drupadia theda*	*Hypolyc. erylus*	*Rapala pheretima*	*Drupadia ravindra*	*Jamides pura*	*Jamides caeruleus*	*Cheritra freja*
1		28	5	2	38	19	>30	34
2		100			2	4		8
3		69						9
4		40						
5		20						
>20	>1000							

rmecoxene *Cheritra freja* to quickly abandon the site (*n* = 5). Females of *A. emolus*, *R. pheretima* and *H. erylus* in most cases, however, landed some distance of the alerted *O. smaragdina* ants, examined the plant surface closely, and fled when an aggressive ant came too close. In contrast to *D. ravindra* and *C. freja* females, they usually returned and resumed their investigation of the plant, often interrupted by approaching ants, until eventually they started to lay their eggs. For oviposition, females of *H. erylus* and *R. pheretima* moved to a part of the hostplant where *O. smaragdina* workers were actually not present. *A. emolus* females, however, predominantly laid eggs near aggregations of *O. smaragdina* ants. The aggressive behaviour of the ants changed when they encountered a female *A. emolus* which had already commenced oviposition. Then the ants peacefully antennated her as well as the freshly laid eggs (Fiedler and Maschwitz 1989b).

Females of the facultative myrmecophiles *D. ravindra* and *Jamides pura* showed no preference for plants inhabited by certain ant species. They also used artificially or naturally ant-free substrates for oviposition. In the specialized flower feeder *Jamides caeruleus*, oviposition only occurred on young inflorescences of *S. thaipingensis*, irrespective of the presence or absence of ants. Females

of the myrmecoxene *C. freja* likewise laid eggs on leaf flushes with or without ants.

While facultatively myrmecophilous or myrmecoxenous lycaenids predominantly deposit their eggs singly, many butterfly species with specific ant-associations and ant-dependent oviposition tend to lay their eggs in clusters (Kitching 1981; Pierce and Elgar 1985). Egg-clustering might help to optimally exploiting the scarce sites where both the specific ant partner and an appropriate hostplant co-occur. In addition, group-living larvae, as a result of egg-clustering, may be more attractive to ants than solitary ones (Pierce et al. 1987, 1991). Table 4 summarizes the information on egg-clutch sizes of our study species.

The egg masses of *A. emolus* are remarkably large (up to 150 eggs, average number 59 eggs per batch, see Fiedler and Maschwitz 1989b). *D. theda* females predominantly lay their eggs in small groups of two to five. Additional to egg-clustering, females of these two obligate and specific myrmecophiles repeatedly use the same part of a plant for oviposition on subsequent days. As a consequence, larvae of *A. emolus* and *D. theda* normally live in groups of variable age.

The yet small number of observations suggests single oviposition in *R. pheretima* and *H. erylus*. The faculta-

Table 5 Outcome of interactions between mature lycaenid larvae and various ant genera investigated under field conditions and in experimentally provoked encounters (numbers of observations given in parentheses) (+ the ants continously tend a larva after an association has been established, and the larva secretes droplets from its dorsal nectar organ which the ants imbibe, 0 the ants mainly ignore the larva, *A* the ants react aggressively after encountering the larva and finally kill it, – neither tested experimentally nor observed in the field so far)

Lycaenid species	*Drupadia theda*	*Anthene emolus*	*Drupadia ravindra*	*Jamides pura*	*Cheritra freja*
Degree of myrmecophily	Obligate myrmecophile	Obligate myrmecophile	Facultative myrmecophile	Facultative myrmecophile	Myrmecoxene
Naturally tended by	*Crematogaster*	*Oecophylla*	Various genera	Various genera	Not attended
Ant genus					
Crematogaster	+(63)	+/A(14)	+(17)	+(18)	0(18)
Acanthomyrmex	0(5)	–	+(6)	+(7)	0(5)
Rhoptromyrmex	0(5)	–	+(5)	+(5)	–
Technomyrmex	0(16)	+(15)	+(24)	+(17)	0(17)
Tapinoma	0(15)	+/0(15)	+(20)	+(17)	0(15)
Iridomyrmex	0(7)	+(5)	+(5)	+(5)	0(5)
Camponotus	0(5)	–	–	–	0(6)
Oecophylla	A (7)	+(47)	A (6)	A (5)	A (8)
Cladomyrma	A (8)	A (10)	A (6)	A (6)	A (6)

Fig. 1 Attractiveness of mature larvae of five lycaenid species towards ants from three different genera, measured as mean number of ants (+ SE) in direct contact with mature caterpillars (5–11 trials per species combination)
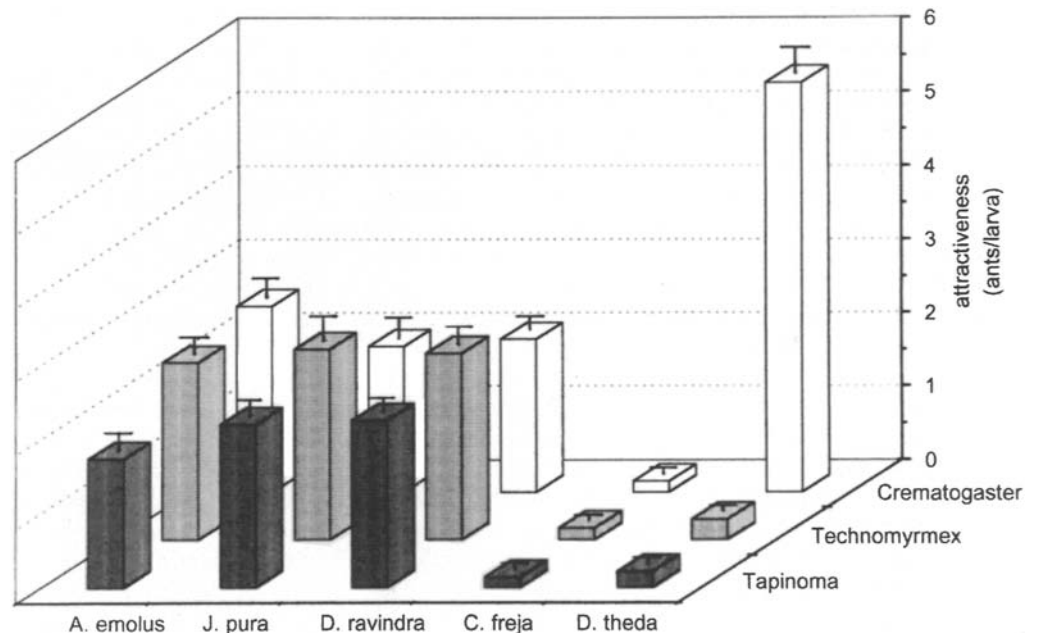
tive myrmecophiles (*D. ravindra, J. pura, J. caeruleus*) as well as the myrmecoxene *C. freja* lay most of their eggs singly, and only exceptionally in small groups. Therefore, the great majority of larvae of the latter four species live solitarily.

Specificity of caterpillar-ant communication and limits of appeasement

The observations on natural ant-associations of lycaenid larvae and oviposition behaviours of female butterflies demonstrate that there occur specific as well as unspecific beneficial relationships between lycaenids associated with *S. thaipingensis* and ants. Furthermore, there are

cases of aggressive interference. As a result, certain combinations of caterpillar and ant species were never encountered in the field. The outcome of experimentally induced interactions between mature larva of five of our study species and various ant genera, which are commonly found in the natural habitat of these lycaenids, are presented in Table 5.

Appeasement did not succeed with all ant species. The extremely aggressive weaver ants (*O. smaragdina*) only accepted caterpillars of *A. emolus* which they also tend in nature. Larvae of other lycaenids were immediately attacked, killed and retrieved as prey. The formicine ant *Cladomyrma petalae*, which inhabits the hollow twigs of some *S. thaipingensis* trees, provides another striking example. Leaf flushes of trees colonized by *C.*

petalae are usually free of lycaenid immatures, and *Cladomyrma* ants attacked and killed all lycaenid larvae which we experimentally placed in reach of them. Only concealed feeders like the larvae of *J. caeruleus* are able to avoid attacks by *C. petalae* and also by *O. smaragdina* through inaccessibility.

Quantitative information on the attractiveness of larvae of these five lycaenid species towards three ant genera obtained in field experiments on *S. thaipingensis* is given in Fig. 1. We made this quantitative approach to detect possible differences in the intensity of the ants' tending behaviour towards different lycaenid species. Larvae of the obligate myrmecophile *D. theda* attracted on average five workers of their specific *Crematogaster* host species, but were largely ignored by other ants. The facultative myrmecophiles *J. pura* and *D. ravindra* were typically visited by only 1–2 ants, and differences in the tending levels were slight and not significant among the two butterfly species with *Crematogaster*, nor in association with *Technomyrmex* or *Tapinoma* (see below). Interestingly, very similar tending levels were achieved by mature larvae of *A. emolus*, which are specific to *O. smaragdina* in nature. The myrmecoxenous *Cheritra freja* larvae were mostly ignored by ants and at most received casual antennation for a few seconds. One-way ANOVA (*Crematogaster*: $F = 308.39$, $P < 0.0001$; *Technomyrmex*: $F = 189.98$, $P < 0.0001$; *Tapinoma*: $F = 156.58$, $P < 0.0001$) followed by Scheffé's multiple comparison (level of significance: $P = 0.05$) revealed three statistical groups with *Crematogaster* [(*D. theda*), (*A. emolus*, *J. pura*, *D. ravindra*), (*Cheritra freja*)] and two statistical groups with *Technomyrmex* and *Tapinoma*, respectively [(*A. emolus*, *J. pura*, *D. ravindra*), (*D. theda*, *Cheritra freja*)].

Discussion

Most previous empirical work on lycaenid butterfly biology, and especially on myrmecophily, has focused on traits of individual species rather than on communities. Primary interest in model species, however, has yielded little progress in unravelling community patterns (Gilbert 1984), although the potential impact of lycaenid myrmecophily on population biology or species diversity has been emphasized repeatedly (Pierce 1984; Hochberg et al. 1994). Therefore, we addressed the question if and how interactions with ants may contribute to maintaining lycaenid diversity in a rather complex assemblage associated with a single hostplant species. Our studies revealed a number of specifically different adaptations to avoid attacks from the more aggressive ants as well as complex and partly contrasting types of peaceful or mutualistic interactions between lycaenids and ants. Collectively, these differences increase the diversity of life history traits among nine lycaenid species sharing a common hostplant species as larval food resource. Thus, our findings corroborate the view that relationships to ants are intimately connected with ecological diversification of lycaenid butterflies (Atsatt 1981; Pierce 1984).

Ants shape the set of lycaenid species associated with *S. thaipingensis* trees mostly in two ways: they influence the colonization of trees by interfering with oviposition behaviour, and subsequently ants play an important role in the establishment and survival of the larvae on their hostplant. With respect to their interactions with lycaenids, two major categories of ants can be distinguished: the more aggressive, dominant and territorial species like *O. smaragdina*, *Cladomyrma petalae* and to some degree *Crematogaster*, and the more opportunistic subdominant ants like *Tapinoma*, *Technomyrmex* and many other genera.

The weaver ant *O. smaragdina* is a keystone predator of immature Lepidoptera in its habitats (Way et al. 1989), while the myrmecophytic ant *Cladomyrma petalae* is highly effective in protecting its hostplants against herbivores (Moog and Maschwitz 1994; P. Seufert and K. Fiedler, personal observation). Both these ant species preclude the colonization of *S. thaipingensis* trees by all but a few specialized lycaenids. *Cladomyrma* ants patrol all leaf flushes of colonized trees and discourage female butterflies from egg-laying. Only the youngest inflorescences, which are not yet intensively patrolled by the ants, are open to oviposition by the flower-feeding specialist *J. caeruleus*. Concealed feeding is a crucial protective life history trait of *J. caeruleus* larvae to escape predation by *Cladomyrma* or *Oecophylla* ants. So, *J. caeruleus* larvae are normally inaccessible to these ants and can develop in their territories, even though workers of both ant species readily killed all *J. caeruleus* larvae offered during experiments. *J. caeruleus* is the only lycaenid butterfly which we so far observed in West Malaysia to break the protective barrier imposed by *Cladomyrma* ants inhabiting *S. thaipingensis* trees.

Larvae of *A. emolus*, *R. pheretima* and *H. erylus* live in specific association with *O. smaragdina*. They successfully appease weaver ants and also a range of other ant genera (Table 5), but fail to do so with *C. petalae*. Females of these three lycaenid species also have evolved behaviours that allow them to lay their eggs in close proximity to their host ants. In contrast, females of other lycaenids rarely lay their eggs in the territories of *Oecophylla*, and none of the caterpillars of such species survived an experimental encounter with weaver ants. As a consequence, hostplants in weaver ant territories have a predictable, unique fauna of associated specialist lycaenid butterflies, but cannot be exploited by myrmecoxenes, unspecialized myrmecophiles, or by obligate myrmecophiles which depend on hosts other than weaver ants.

The three lycaenid species associated with *Oecophylla*, as well as the concealed feeder *J. caeruleus* probably live in a relatively enemy-free space (Atsatt 1981), because they colonize trees inhabited by hostile ants, where few competitors or predators of lycaenid immatures should be able to establish. Furthermore, *Oecophylla* ants might actively defend their trophobiotic lycaenid partners against predators and/or parasitoids, as has been shown for a couple of other lycaenid species (e.g.

Pierce and Easteal 1986; Pierce et al. 1987) and in a number of ant-homopteran interactions (Way 1963).

The specializations, however, which allow *A. emolus*, *R. pheretima*, *H. erylus* and *J. caeruleus* to evade fatal attacks of the more aggressive ant species restrict the number of habitats to be colonized. Larvae of *J. caeruleus* feed only on inflorescences in nature, although they readily accept young leaves in the laboratory. Flowering in *S. thaipingensis* does not occur continuously throughout the year (P. Seufert and K. Fiedler, personal observation), and therefore *J. caeruleus* populations probably pass through periods when resource availability might severely limit population size. When egg-laying, females of the three lycaenids specifically associated with *O. smaragdina* have to search for the patchily distributed sites where appropriate hostplants and weaver ants co-occur.

Drupadia theda, with its obligatory and specific association with two *Crematogaster* species, faces the same kind of disadvantage, i.e. restriction of the plant resources which can actually be utilized. Compared to *O. smaragdina* or *Cladomyrma petalae*, *Crematogaster* ants are less aggressive. They also tend facultative myrmecophiles and even tolerate myrmecoxenous caterpillars. *D. theda* larvae benefit through protection by their specific ant partners against parasitoids and most probably against some kind of flying predators (P. Seufert and K. Fiedler, to be published). The efficiency of such protection might increase with the number of ants tending each caterpillar. Therefore, specialized and optimized larval communication signals, which increase the caterpillars' attractiveness towards their ant partners, could improve protection against natural enemies. Our experiments showed that larval signals of *D. theda* are in fact specialized to communicate with *Crematogaster* ants. Yet, this increase in communicative efficiency further restrains *D. theda* immatures to those patchily distributed hostplants which are inhabited by their appropriate host ants.

Facultatively myrmecophilous (*D. ravindra*, *J. pura*) or myrmecoxenous lycaenid larvae (*Cheritra freja*) effectively appease a broad range of less dominant and less aggressive ants (e.g. *Crematogaster*, *Technomyrmex*, *Tapinoma*), which commonly forage at extrafloral nectaries of *S. thaipingensis*. Therefore, these butterflies may opportunistically colonize all suitable hostplants except those trees protected by territorial *Oecophylla* or *Cladomyrma* ants. Females of these species do not depend on ants during their search for oviposition sites; a suitable part of a hostplant alone is sufficient to induce egg-laying.

Facultative myrmecophiles with their unspecialized signals to communicate with ants attract a smaller number of ants per individual larva compared to obligate myrmecophiles in association with their specific ant partners (Fig. 1). Therefore, protection against predators and parasites might be less effective in facultative myrmecophiles. For example, ant protection is of paramount importance in obligately myrmecophilous butterflies like *Jalmenus evagoras* (Pierce et al. 1987) or *D. theda* (P.

Seufert and K. Fiedler, to be published), but considerably less pronounced and not universally detectable in facultative myrmecophiles (Pierce and Easteal 1986; DeVries 1991b; Peterson 1993; Wagner 1994). Finally, myrmecoxenous caterpillars, like those of *Cheritra freja*, probably gain no active protection against predators and parasites, although they likewise enjoy a comparatively enemy-free space on their EFN-bearing, ant-foraged hostplants.

If ant-protection is lower or even absent in facultative myrmecophiles and myrmecoxenes than in specialized myrmecophiles, the former require alternative mechanisms of enemy escape. One important trait might be to lay eggs singly (Table 4), which results in low density of caterpillars. Solitary dispersed larvae are more difficult to locate for predators or parasitoids than the groups of gregarious *A. emolus* or *D. theda* larvae. Conversely, attendant ants may even serve as oviposition cues for parasitoids of obligate myrmecophiles (Nash 1989). On the other hand, the low-density strategy of facultative myrmecophiles or myrmecoxenes limits the rate of exploitation of suitable hostplants. Another peculiar mode of defence is found in the myrmecoxene *Cheritra freja*, whose bizarre larvae bear long, sharply pointed dorsal and lateral tubercles. These protuberances protect the caterpillars against attacks by polistine wasps, whereas other lycaenid larvae are often retrieved as prey by such predators (P. Seufert, unpublished observation).

Saraca thaipingensis is an ant-defended plant species with two complementary modes of mutualism with ants. EFNs on leaf flushes unspecifically attract a broad range of ant taxa, which most probably reduce the high herbivore pressure on the nutrient-rich young foliage. Furthermore, a fraction of trees (about 10–20% at Gombak riversides) is inhabited by *Cladomyrma* spp. ants which specifically nest inside the hollow twigs (Maschwitz et al. 1991). This more advanced myrmecophytic association between *Cladomyrma* and *S. thaipingensis* turned out to be effective in preventing herbivory (Moog and Maschwitz 1994). Only *J. caeruleus* is able to survive on such plants due to its concealed life-habits. Even in laboratory encounters, *Cladomyrma* ants never tended lycaenid immatures. Apparently, their specific adaptations to myrmecophytism have led these ants away from the basic communication pathways which usually underly trophobiotic symbioses between ants and lycaenids or homopterans. In this respect, *Cladomyrma* ants are more effective against herbivores than the ant partners in certain other myrmecophytic associations, where specialized lycaenid butterflies are able to integrate into the ant-plant mutualism (Maschwitz et al. 1984).

The various other ant taxa attracted to EFNs, in contrast, do not protect *S. thaipingensis* trees from lycaenid herbivory. Obligate myrmecophiles are even drawn to plants foraged by their specific host ants. The damage on leaf flushes of *S. thaipingensis* trees caused by specific myrmecophiles like *A. emolus* or *D. theda* is particularly intense and occasionally leads to complete defoliation of branches or entire small trees (K. Fiedler and P. Seufert,

personal observation). Utilization of EFN plants by herbivorous myrmecophiles is known from a couple of riodinid (Horvitz and Schemske 1984; DeVries 1991a) or lycaenid butterfly species (Fiedler 1992). In addition, the ant-tended caterpillars may benefit from their ant guards (DeVries 1991b) and may utilize also extrafloral nectar as additional nutrient resource (DeVries and Baker 1989). Hence, facultative EFN-mediated ant-plant mutualisms are open to exploitation through ant-tended butterfly larvae (such mutualisms may even be a preferred resource: DeVries 1991a).

Our work on the lycaenid butterflies associated with *S. thaipingensis* revealed multiple facets to how ants may shape a set of coexisting lycaenid species via predator-prey interactions, different types of lycaenid-ant mutualisms, coexistence of butterflies and ants mediated by appeasement strategies, and trade-offs with ant-plant symbioses. Among obligate myrmecophiles resource partitioning is partly determined through relationships with specific ants. The peculiar ecology of territorial *Oecophylla* and *Cladomyrma* ants also determines the colonization of *S. thaipingensis* trees by lycaenids. Adaptations to evade fatal attacks by aggressive ants and the restriction to habitats colonized by less dominant ants characterize the facultative myrmecophiles and myrmecoxenes. Apart from these deterministic predictable interactions, we also found stochastic components in the patterns of colonization. Among lycaenids which share common ant partners, be it obligate myrmecophiles associated with weaver ants or facultative myrmecophiles in symbiosis with a range of less dominant ant genera, the actual representation of the members of each subset on a given suitable *S. thaipingensis* tree remains unpredictable. Hence, colonization and establishment of the lycaenid butterfly species associated with the hostplant tree *S. thaipingensis* are goverened by a mixture of mechanisms, where interactions with ants play an important role in maintaining a diversity of life-cycle patterns.

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