0014-4754/96/010014-11$1.50 + 0.20 © Birkhäuser Verlag Basel, 1996

Butterflies and ants: the communicative domain

K. Fiedler, B. Hölldobler and P. Seufert

Theodor-Boveri-Institut am Biozentrum der Universität, Lehrstuhl für Verhaltensphysiologie und Soziobiologie, Am Hubland, D-97074 Würzburg (Germany), Fax +49 931 888 4309

Received 28 March 1995; accepted 8 June 1995

Abstract. Associations with ants, termed myrmecophily, are widespread in the butterfly family Lycaenidae and range from mere co-existence to more or less specific mutualistic or even parasitic interactions. Secretions of specialized epidermal glands are crucial for mediating the interactions. Transfer of nutrients (carbohydrates, amino acids) from butterfly larvae to ants plays a major role, but manipulative communication with the help of odour signals is also involved. By means of myrmecophily, lycaenid butterflies largely escape ant predation, and certain species gain protection through attendant ants or achieve developmental benefits from ant-attendance. Benefits to the ants range from minimal to substantial food rewards. While most lycaenid species maintain facultative relationships with a variety of ant genera, highly specific and obligatory associations have convergently evolved in a number of butterfly lineages. As a corollary, communication systems are largely unspecific in the former, but may be highly specialized in the latter. The sophisticated communication between obligate myrmecophiles and their host ants is tightly connected with the evolutionary rise of specialized life-cycles and thus is a source of augmenting diversity within the butterflies.

Key words. Lycaenidae; Formicidae; symbiosis; mutualism; parasitism; communication; ecology; evolution.

In most terrestrial ecosystems, social insects like ants, termites, and many wasps or bees, make up a significant part of the animal life[125]. Ants, in particular, are not only dominant in terms of abundance and biomass, but also are the leading invertebrate predators[62]. Keystone ant species often play a prominent role in shaping and structuring whole arthropod guilds and faunas[16,66,74,78,101,123,126]. Not surprisingly, a large number of animals, the so-called myrmecophiles, have evolved to utilize these omnipresent hymenopterans or their nests as resources[62,72].

Ants utilize highly sophisticated (mostly chemical) means of communication, by which they operate complex systems of division of labour and which enable them to discriminate effectively between nestmates and alien competitors[62]. Hence, to evolve into a myrmecophile by necessity requires the ability to break the ants' communication codes. Myrmecophilous arthropods employ a broad array of strategies to deal with their hosts[9–11,57–61,63,64,117]. We here use a particular example to illustrate the fascinating diversity of interspecific communicative phenomena and their ecological ramifications: the butterfly family Lycaenidae (fig. 1).

Soft-bodied slowly moving caterpillars of butterflies and moths are classical prey organisms of ants[66,68,74,104]. Therefore, the occurrence of non-aggressive associations between the larvae of lycaenid butterflies and ants is a startling paradigm of interspecific communication. How do caterpillars circumvent ant attacks? And how do ants recognize caterpillars as non-prey? Furthermore, interactions between lycaenids and ants are by no means restricted to the larval stages, but may occur during any part of the life-cycle from the egg to the adult, and butterfly-ant relationships cover the whole continuum from mutualism to commensalism and even parasitism[35]. Myrmecophily among Lycaenidae butterflies has attracted naturalists since the discovery of the first examples at the end of the 18th century[31,54,67,75,122], but with the development of new theoretical concepts in behavioural ecology the phenomenon has been explored in numerous directions as a model for the ecology and evolution of interspecific interactions[3,17–21,35–37,55,56,88–98,113,114,116]. In this essay, we first focus on commu-

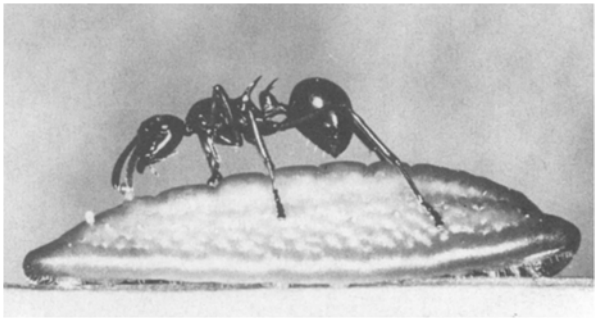

Figure 1. Mature caterpillar of the South East Asian lycaenid butterfly, *Eooxylides tharis*, tended by a *Myrmicaria* worker ant. The caterpillar (length ca. 14 mm) offers a nutrient-rich secretion droplet from the dorsal nectar organ and simultaneously everts the whitish membraneous tentacle organs. (Photograph: K. Fiedler.)

nicative processes involved in caterpillar-ant relationships. Then, we turn briefly to the other stages in the butterflies' life cycle and we will draw some parallels with other myrmecophiles. Finally we touch on ecological and evolutionary patterns.

Mutual recognition of partners

When a foraging ant encounters a lycaenid caterpillar which is feeding or resting on its hostplant, the primary decision of the ant is whether or not to attack the caterpillar as prey. Lycaenid caterpillars use a number of signals to manipulate this decision. Most important are chemical signals emitted from specialized epidermal glands, the so-called myrmecophilous organs (fig. 2)[13,79]. Although the chemistry of these secretions is still barely explored, many behavioural observations and experiments demonstrate that they play an important role in the interspecific interactions. Almost all lycaenid larvae possess minute, hair-derived glands ('pore cupola organs') which are scattered over the surface or concentrated at taxon-specific locations. During encounters, ants intensively antennate these glands and press their mouthparts onto these organs, apparently collecting the secretions[79]. The same individual caterpillar may be attended at different times by a variety of ant species belonging to different subfamilies[87]. On the other hand, not all lycaenid caterpillars equipped with pore cupolas release antennation behaviour of equal intensity. Some species elicit little attraction in ants, while others receive constant antennal drumming[5,35,79].

Since the response of ants usually starts after initial tactile contact with a caterpillar, we assume that the chemical signals are of low volatility[88]. Malicky[79], who first demonstrated the glandular nature and behavioural significance of the pore cupolas, suggested that their secretions resemble ant-brood signals. Later, the substances were categorized as either 'adoption'[88] or 'appeasement' signals[83]. Chemical evidence is still scant, but suggests that amino acids are secreted by some species[92] and mimics of brood pheromones by others[51,114].

Based on the morphology of the pore cupolas, we assume their secretions permanently percolate through the pores in the sieve plate where they accumulate. Furthermore, other hair-derived structures like dendritic setae[5] (also Fiedler, unpublished) receive particular antennation by ants and are strongly suspect of being glands involved in myrmecophily. As a consequence, even during moult phases (e.g. pupation) caterpillars often remain highly attractive to ants. Freshly killed caterpillars (e.g. after deep-freezing: Fiedler, unpublished), or larval carcasses after the emergence of parasitoids[48], or pupal cases after the imago has emerged, retain their attractiveness for hours or days. Obviously, the 'adoption' or 'appeasement' components involved in caterpillar-ant communication are quite persistent and continuously present signals.

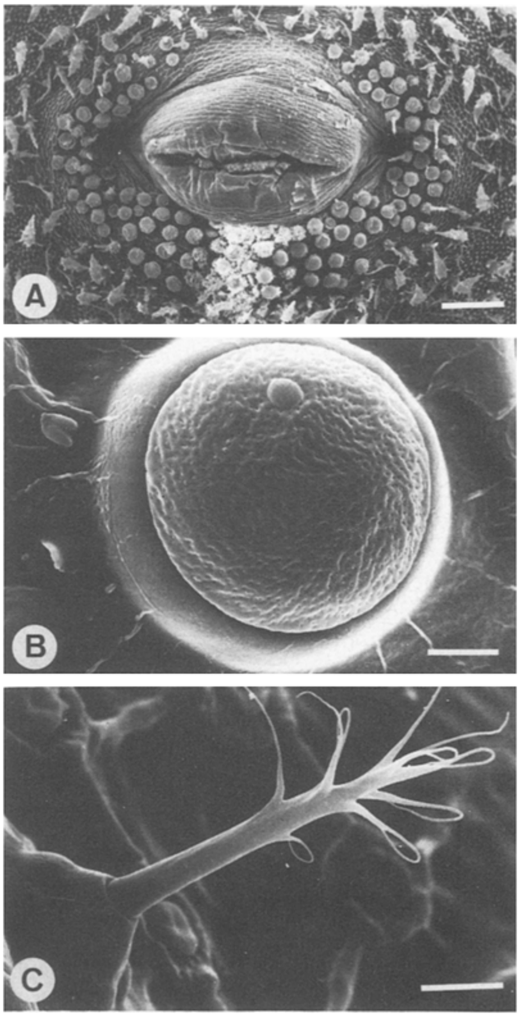

Figure 2. Myrmecophilous organs of lycaenid immatures involved in butterfly-ant communication. *A* The half-everted dorsal nectar organ of a mature larva of *Jamides virgulatus* from Malaysia. The gland opening is surrounded by secretory pore cupola organs and mechanoreceptive setae of peculiar shape. Scale: 100 µm. *B* Pore cupola organ of a pupa of *Polyommatus thersites* from central Europe. The hair shaft of this type of setae is transformed into a sieve-plate with numerous minute pores, through which secretions attractive to ants are emitted. Scale: 5 µm. *C* A dendritic seta on the pupa of *Jamides talinga* from Borneo. Dendritic setae of myrmecophilous caterpillars or pupae receive intensive antennation behaviour in attendant ants. Scale: 10 µm. (Photographs: A. Gerber/K. Fiedler.)

Other signals are produced in discrete units. Most myrmecophilous lycaenid caterpillars possess a glandular dorsal nectar organ. After antennal drumming around the gland opening[79], the caterpillars deliver droplets of an aqueous solution rich in carbohydrates and/or amino acids to their attendant ants[15,84,88,121]. The nectar-like secretions provide ants with small, but nevertheless valuable amounts of nutrients[41,86,97]. Ants encountering the nectar-like secretions often recruit nestmates to the caterpillars[43], thereby monopolizing the food resource and stabilizing the caterpillar-ant association. The caterpillars also offer nectar droplets when attending ants sometimes behave aggressively[79], or when a caterpillar with a stable ant-association is experimentally harassed (imitating a predator's attack[77]; also Fiedler, unpublished data).

Many myrmecophilous caterpillars possess eversible tentacle organs equipped with finely branched setae on top. These organs are located just behind the nectar gland. These membraneous tentacles are most frequently everted when a caterpillar-ant interaction commences[7,17,39,65], when caterpillars are travelling from feeding to resting places[12,50,51], or when caterpillars are disturbed[77]. The attendant ants react to such tentacle waving by running around and over the caterpillar with increased speed[5,42] or they may even jerk towards the everted tentacles, which are immediately withdrawn whenever touched. Although supporting chemical evidence is available for only one South African *Aloeides* species[51], the commonly observed alert behaviour of ants in response to tentacle eversions suggests that these structures emit volatile substances which may mimic short-range alarm pheromones of the ants.

In addition, caterpillars[18,19,22] and pupae[24,25] of Lycaenidae and Riodinidae butterflies produce substrate-borne vibrations. DeVries[18] observed that stridulating caterpillars of the Neotropical riodinid butterfly *Thisbe irenea* were attended by a larger group of ant guards than larvae experimentally rendered mute. Recent work on European lycaenid species revealed that vibratory signals do not attract a larger number of ants over a distance, but rather accelerate and stabilize the establishment of caterpillar-ant associations, presumably by modulating the recruitment process (Wieland and Fiedler, unpublished data). Although the significance of vibratory communication in myrmecophilous interactions has been documented in only a few species, and such vibrations may also have other, not yet known functions, it seems safe to conclude that immatures of myrmecophilous lycaenid and riodinid butterflies use mechanical, as well as a variety of chemical, signals and nutrient rewards to prevent ants from attacking.

Thus, lycaenid butterflies employ a complex set of communicative signals to gain acceptance by ants. In contrast, the means by which caterpillars recognize the ants appear to be much simpler. Most lycaenid larvae do not actively seek out their ant mutualists, but wait for the ants to come. Specialized mechanoreceptors located around the dorsal nectar organ of the caterpillars, which allow a fine temporal resolution of tactile stimulation patterns[111], are used to distinguish between antennal drumming of ants or tactile stimulation by other insects. These receptors can sometimes be fooled, however, by experimental stimulation[26], and insects like thysanopterans, lycaenid adults or braconid wasps[23,49,107] have been observed to 'steal' secretions from the nectar organ by stimulating it with their mouthparts or antennae.

More specific recognition of appropriate host ants has rarely been documented among myrmecophilous lycaenids. Though some myrmecophilous insects and snakes locate their host ants by following the ants' pheromone trails[10,11,62,100,124], for lycaenids this has only been conclusively demonstrated in the Australian obligate myrmecophile *Jalmenus evagoras*[85]. Other cases where trail following had been suspected later proved to be inconclusive or erroneous[33,106]. However, there are numerous anecdotal reports of apparent trail following behaviour in tropical obligate myrmecophiles[50], which deserve to be studied in greater detail. In particular, it must be tested experimentally whether lycaenid larvae just follow their own silk trails or really respond to the ants' trail pheromones. Preferential pupation inside ant nests has also been reported[27,121], but this needs to be verified by additional observations. It is likely that in the course of future research more cases of orientation using ant-derived chemical cues will be found among the caterpillars or adults of myrmecophilous Lycaenidae.

Caterpillar signals: honesty or deceit?

Do caterpillars honestly signal their value as a trophobiotic partner? Or do they deceive and manipulate ants by fobbing them off with negligible pseudo-rewards? This is important with respect to the evolutionary stability of caterpillar-ant associations. Detailed cost-benefit analyses exist for only a small number of lycaenid species, but these suggest that lycaenids employ honest signalling as well as chemical manipulation. Caterpillars of the Australian hairstreak species *Jalmenus evagoras*[86,97] and the Western Palearctic blue butterfly *Polyommatus coridon*[41] produce secretions in amounts large enough to contribute substantially to the nourishment of ants. Experiments with ants being caged with lycaenid immatures[15] (also Fiedler and Saam, unpublished data) likewise showed that ants survived better when they had access to the nectar-like secretions of myrmecophilous caterpillars. Lifetime investment of caterpillars in nectar secretions has been estimated for a couple of species, based on extensive studies of their secretory behaviour[7,39,41,47,65], and these estimates also confirm that caterpillar secretions may contribute to the food supply of ants. Accordingly, given the beneficial effects of ant-attendance on caterpillar survival[21,93,95,97] (also Seufert and Fiedler, unpublished data) or growth[15,40,46,65,120], associations between lycaenid larvae and ants are at least potentially mutualistic.

Besides the attractive odour of caterpillars, their tentacle organs may provide honest signals. Larvae of *Polyommatus icarus*[77] and *P. coridon* (Fiedler, unpublished data) evert their tentacles in response to simulated predator attacks and simultaneously offer an additional nectar droplet. Hence, such caterpillars alert their ant guards and immediately reward them with food. Tentacle eversion rates in myrmecophilous larvae of *P. icarus* and *Aricia agestis* are significantly correlated with their secretory capacity[7,65], though such correlations were absent or unstable in experiments with other species[35,39]. In addition, lycaenid species whose larvae produce nectar secretions at high rates, like the strongly ant-associated *Polyommatus coridon*, generally evert their tentacles more frequently than moderately myrmecophilous species like the congeneric *P. icarus*[35]. These observations seem to suggest that one function of the tentacle organs is to advertise the profitability of a caterpillar and to direct the attendant ants towards the nectar source, although this does not apply to all lycaenid species[12].

On the other hand, lycaenid caterpillars use a variety of strategies to minimize their investment in myrmecophily. After the initial phase of an encounter, secretion rates and tentacle eversion frequency rapidly decrease as soon as a stable caterpillar-ant association has been established[7,39,65]. Such a process, termed 'enticement and binding' by DeVries[17], shows that manipulative elements are involved in these facultative mutualisms: with time caterpillars apparently substitute odour for food rewards. Furthermore, caterpillars finely adjust their secretion rates according to the number of ants present, the stability of their ant-association, their developmental status and the resources available from their food plants[6,7,34,36,39,65,90,98]. Accordingly, caterpillars of the same lycaenid species exhibit a remarkable temporal or individual variability with regard to their profitability as food resource for ants[98], and this is often reflected in the ants' reaction. Caterpillars of *Glaucopsyche lygdamus*[93], *P. icarus*[34] or *Jalmenus evagoras*[6], which had been fed nutrient-poor diets, attracted fewer ants than those on favourable food. Nevertheless, food-constrained larvae of *P. icarus* (e.g. if reared on foliage instead of flowers of their hostplants) are still able to induce long-lasting associations with *Lasius* ants in the laboratory[7].

From the energetic point of view, tending instead of consuming a caterpillar is profitable for the ants only if the ant colony can derive a larger reward from harvesting the secretions than from consuming all caterpillars that the worker ants encounter. This conflict is further enhanced by the foraging costs which ants experience when tending caterpillars (costs of travel between nest and feeding place, mortality risks while outside the nest). The dimension of this conflict is difficult to estimate. In many lycaenid species myrmecophilous interactions occur from the third larval instar onwards, when all myrmecophilous organs have become functional[35,79]. The fresh weights of such larvae typically range from 2–5 mg with a water content of 80–90%. The corresponding dry mass of 0.2–1 mg contains lipids, proteins and carbohydrates in unknown ratios. If this dry mass were entirely proteins and carbohydrates, its energy content (calculated as thermic equivalent) would be 3–17 J, and 7–39 J if the caterpillar consisted only of fat body. These figures cover the same range as estimates of the carbohydrate-based energy content of nectar secretions which can be harvested over the lifetime of an individual caterpillar (3–70 J[7,39,41,44,47,65]). The latter figures are underestimates, because amino acid components in the nectar or pore cupola secretions[15,88,92,121] were not considered.

Nevertheless, the nutritive benefits accruing to ants from tending lycaenid immatures apparently do not much exceed those they could gain from consuming the larvae. It must be taken into account, however, that more significant benefits could be obtained on the long term. Through tending, ants can decrease caterpillar mortality, and thus increase population size, in comparison to non-tended prey species[93]. Eventually, this might lead to a predictable net benefit over the years for long-lived superorganisms like ant societies.

The above crude energetic argument provides two alternative, but not mutually exclusive, explanations for why ants do not attack lycaenid caterpillars. Either the caterpillar secretions contain components (e.g. particular amino acids) which are so essential for the ants' diet that even the delivery of relatively small quantities in the secretions is beneficial; or the 'adoption' or 'appeasement' signals are sufficiently close to the chemical code of the ants (e.g. to brood odour components) to serve as effective mimics. In the latter case, there would be little opportunity for selection against this type of 'fooling', since the worker ants' fitness essentially depends on their caring for brood[62] and, therefore, gives little selective leverage to the ants to abandon tending behaviour.

This leads to an unresolved question in the mechanistic analysis of trophobioses in ants in general. Be it lycaenid caterpillars or honeydew-excreting homopterans, an essential part of all their symbiotic interactions with ants is the avoidance of fatal ant attacks. The chemical nature of the appeasement or adoption substances is almost unknown. Nevertheless, they are obviously effective across an amazing taxonomic range of different ant subfamilies and of trophobionts from several insect orders. Most likely, therefore, these signals are very simple basal components of the ants' odour language. Evidence from adoption experiments with ant brood suggests that brood odours also contain, besides more specific signals, unspecific compounds which sometimes allow for adoption of larvae even across subfamily borders[62]. Trophobionts may have evolved to communicate with such basal signals, whereas advanced highly integrated myrmecophiles, like many beetles, have specifically adapted to break their host ants' species-specific code[57–61,63,64,117]. The chemical identification of generalized as well as specialized adoption signals will obviously make a major contribution to our further understanding of myrmecophilous interactions in general.

The family Lycaenidae contains a considerable number of species in various taxonomic groups whose larvae possess only pore cupolas, and sometimes dendritic setae, but not a dorsal nectar organ. Such 'myrmecoxenous' lycaenids[35,73] are usually not attacked during interactions with ants. After an initial phase of more or less intensive antennation[5,79], myrmecoxenous caterpillars are usually abandoned by the ants, but occasionally associations may last for some time[35]. Similarly, lycaenid pupae do not possess a nectar organ (but see[53,119]), but are often highly attractive to ants and may induce stable, long-lasting symbiotic associations through the release of recruitment behavior[32,43]. Due to the lack of nectar-like secretions, worker ants soon die if caged exclusively with pupae or myrmecoxenous larvae (Fiedler and Saam, unpublished data). Thus, at least in these cases the secretion of appeasement or adoption substances is clearly manipulative: ants gain little benefit from harvesting the secretions, while the lycaenid immatures escape ant predation. It remains to be ascertained whether pupae or myrmecoxenous larvae of lycaenid butterflies may even benefit from the ants' protection against other predators or parasitoids.

Specificity of interactions

As already stated, the majority of myrmecophilous relationships observed in the butterfly family Lycaenidae are not specific with respect to the ants involved. Furthermore, not all individuals in a population are tended by ants in nature, and the immatures are able to develop and survive without attendant ants. These species are termed **facultative myrmecophiles**, and the degree of such associations ranges within wide limits from very occasional interactions to species whose caterpillars are almost invariably tended[35].

A number of lycaenid species, however, have evolved to become **obligate myrmecophiles**. These are specifically bound to a particular host ant species or genus[35], and survival without ants is almost impossible due to intense predation[97] (also Seufert and Fiedler, unpublished data). Some obligate myrmecophiles spontaneously deliver secretions in such large amounts that they die from fungal attack in captivity if deprived of their ant partners (Seufert and Fiedler, unpublished data). Such close and obligate symbioses require that strategies have been evolved to locate and select the correct ant host. The most common way is that adult female butterflies search for the appropriate host ant (fig. 3), when selecting oviposition sites[4,44,45,70,71,94,108,110]. There exists some evidence that ant pheromone trails are used as recognition cues[50,51], although visual orientation cannot be excluded. During oviposition, the females are often antennated by their host ants, but in many cases these encounters are totally unaggressive[45,82,108], suggesting that the adult butterflies also have some chemical appeasement signal. In the Oriental *Anthene emolus*, the host ant *Oecophylla smaragdina* initially tries to attack alighting females, but as soon as oviposition has commenced, ant aggression ceases[44]. Here, the freshly laid eggs apparently disseminate the appeasement signal.

Figure 3. A female butterfly of the South East Asian obligate myrmecophile, *Drupadia theda*, has laid an egg (white arrow) while being antennated by a worker of its specific *Crematogaster* host ant. (Photograph: P. Seufert.)

If the specificity of an ant-association is initiated by the egg-laying female, what about the communication signals in the subsequent larval or pupal stage? Ongoing studies on obligate myrmecophiles in South East Asia have revealed a variety of opportunities. Caterpillars of the aforementioned *A. emolus* are always tended by *Oecophylla smaragdina* in nature, but associations with a couple of different ant genera could experimentally be established. These 'alien' ants intensively antennated the caterpillars and imbibed the nectar secretions (table 1). Caterpillars of two other obligate myrmecophiles (*Rapala dieneces* and *Drupadia theda*), in contrast, were totally ignored when caged with the 'wrong' ants. In the case of *D. theda*, the ants even neglected a nectar droplet provided by the larva. Hence, some obligatorily myrmecophilous caterpillars use highly specific odour signals and may even have adapted their food rewards to their specific partners. Studies of certain temperate-zone species suggest a similar specificity between ants and lycaenids[69]. On the other hand, specializations in the larval communication signals are not a necessary character of obligate myrmecophiles.

Table 1. Outcome of interactions between mature lycaenid larvae and various ant genera.

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 specific to	*Crematogaster*	*Oecophylla*	unspecific	unspecific	unspecific
Ant genus					
Crematogaster	+	+/aggr.	+	+	0
Acanthomyrmex	0	–	+	+	0
Rhoptromyrmex	0	–	+	+	–
Technomyrmex	0	+	+	+	0
Tapinoma	0	+/0	+	+	0
Iridomyrmex	0	+	+	+	0
Camponotus	0	–	–	–	0
Oecophylla	aggr.	+	aggr.	aggr.	aggr.
Cladomyrma	aggr.	aggr.	aggr.	aggr.	aggr.

In Peninsular Malaysia, at least ten lycaenid species utilize the legume tree *Saraca thaipingensis* as larval hostplant. The interactions between the five more common species of these butterflies and representative abundant ants were investigated under field conditions and in experimentally provoked encounters. The abbreviations denote the following behaviours:

+: the ants continuously tend the 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.

aggr.: the ants react aggressively after encountering the larva and finally kill it.

–: neither tested experimentally nor so far observed in the field.

The Palearctic genus *Maculinea* has a highly specialized life-cycle. Caterpillars feed inside flowers of specific hostplants throughout the initial three larval instars. Then, in the final instar, they leave their hostplant and are carried by *Myrmica* ants into the nests, where the caterpillars turn into predators of ant brood or solicit trophallaxis from their host ants[28–30,55,56,112–116]. Surprisingly, this adoption appears to be a relatively haphazard process, despite the fact that *Maculinea* caterpillars fully depend on arriving in an appropriate host ant nest. An earlier claim that caterpillars would actively search and follow the ants' pheromone trails[106] has never been confirmed[33,112]. From observations of oviposition behaviour, there is also no solid evidence that *Maculinea* females respond to the presence of *Myrmica* ants during egg-laying[33,112]. Nevertheless, *Maculinea* eggs tend to be clumped on hostplants where the appropriate specific *Myrmica* hosts are abundant[105]. It remains to be tested whether this spatial association is really the result of host recognition, or whether the females use environmental variables (such as vegetation density or height, microclimate) which are correlated with the preferred habitat of the specific *Myrmica* species. In *Maculinea*, adoption can occur with any *Myrmica* species, but once in the nest the caterpillars only survive if housed with a specific *Myrmica* host species[114]. Hence, adoption is genus-specific (most likely governed by brood-pheromone mimics), whereas subsequent permanent acceptance requires a finer matching of signals[22,29,30,113,115,116].

The limits of appeasement

The preceding *Maculinea* example raised the question of whether their myrmecophilous signals exempt lycaenids from all ant predation. This is not the case. Ant predation occurs, for example, in certain obligate myrmecophiles if these are found by the 'wrong' ants[103]. Certain *Formica* wood ants show a greater tendency to attack lycaenid larvae than others[79,80]. In Malaysia, we observed that weaver ants (*Oecophylla smaragdina*) only accepted those caterpillar species which associate with this ant in nature. Other species were immediately attacked and killed when offered in experiments (fig. 4). The formicine ant *Cladomyrma petalae*[2] provides another striking example. This ant species lives in the hollow twigs of myrmecophytic *Saraca thaipingensis* (Caesalpiniaceae) trees[81], but not all these trees are actually colonized. While trees without *Cladomyrma* ants frequently serve as hostplants for at least ten lycaenid species in Peninsular Malaysia, colonized trees are usually free of lycaenid immatures (Seufert and Fiedler, unpublished). Without a single exception, *Cladomyrma* ants attacked and killed all lycaenid larvae experimentally placed on leaf flushes of *S. thaipingensis*. Only one lycaenid species whose larvae bore inside the inflorescences escapes ant predation by inaccessibility.

These examples reveal that communication with, and 'manipulation' of, ants by lycaenid butterflies requires a subtle balance between the investment in communication signals and food rewards on the one hand, and the range of target ants on the other. Unspecific signals prevent a large guild of ants from attacking. Specific signals may fail towards the 'wrong' addressee. And certain ants with particular life cycles, like the *Cladomyrma* species involved in myrmecophytism, may be refractory to all attempts at deceit.

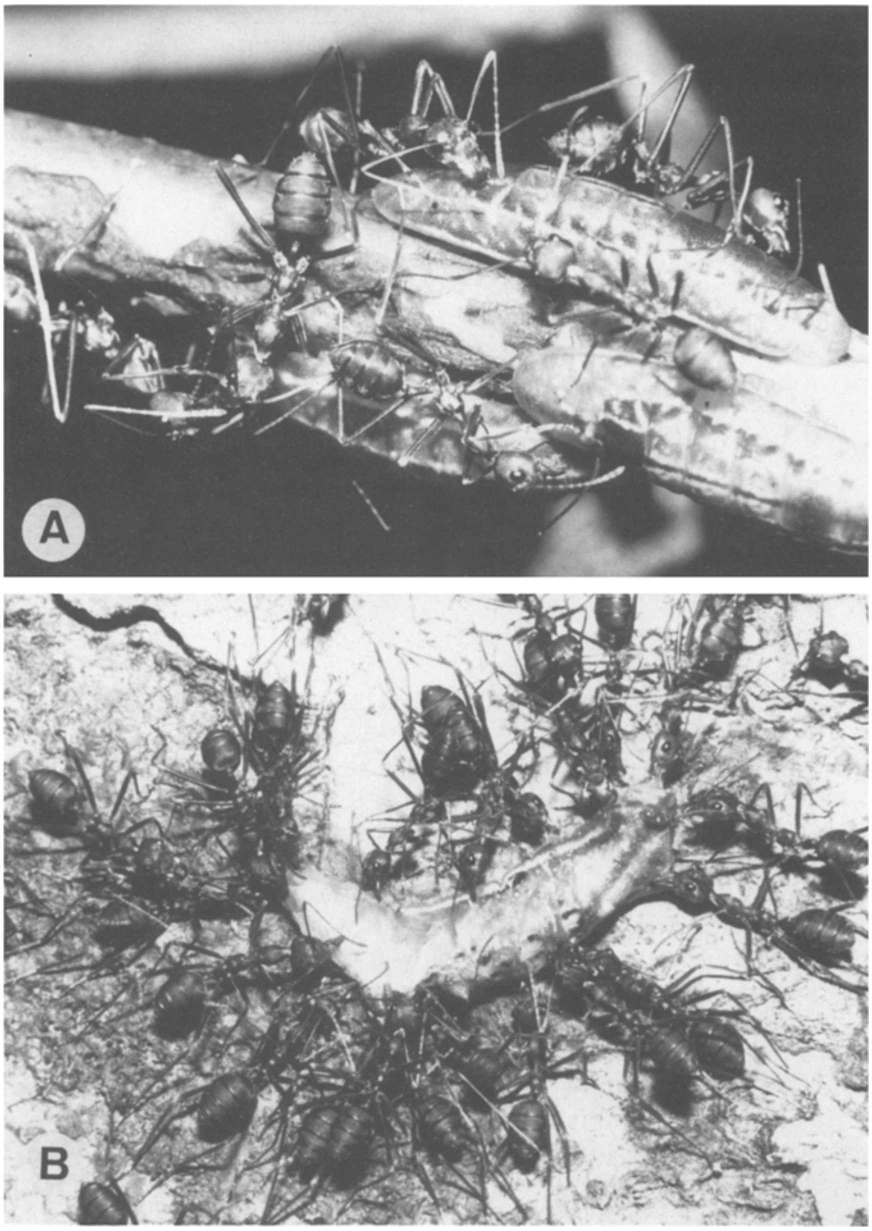

Figure 4. Interactions between South East Asian weaver ants (*Oecophylla smaragdina*) and lycaenid butterfly larvae with contrasting results. *A* A group of mature larvae of the obligate myrmecophile *Anthene emolus* is permanently attended by ant guards which defend the caterpillars against enemies. *B* Upon encounter, the larva of the non-myrmecophilous species *Cheritra freja* is immediately attacked and killed by a group of cooperating ants. In this case the communication between caterpillars and ants fails completely. (Photographs: P. Seufert.)

Diversity of communication: an avenue to species diversity?

At present, systematists have recognized some 4500 species of Lycaenidae butterflies (excluding the Riodinidae[109]), and the total species diversity is likely to be in the range of 5000–6000[52]. Far more than half of these live in some kind of association with ants at least during part of the life cycle[35,91], and even the non-tended myrmecoxenous species do communicate with ants in some way, as evidenced by their ability to appease ants in encounters. It is thus tempting to assume that communication with ants has played a role in the rise of species diversity in that butterfly family[89,118]. A conclusive answer is out of reach, but in certain cases the importance of communication with ants is obvious.

Lycaenid larvae which enter ant nests to live there as predators of ant brood or commensals could never gain access to those niches without appropriate communication signals. Therefore, the multiple evolution of such aberrant life cycles among the normally phytophagous butterflies[1,13,14,35] is closely connected with the evolution of highly specialized interspecific communication and has clearly added to the current diversity. Although not that numerous, there are some 30 species in which obligate non-mutualistic, and mostly parasitic, inquilinism has been documented (scattered over the genera *Allotinus*, *Thestor*, *Liphyra*, *Euliphyra*, *Aphnaeus*, *Spindasis*, *Cigaritis*, *Oxychaeta*, *Acrodipsas*, *Maculinea*, *Lepidochrysops* and others[8,13,14,35,76,82,102,114], also Sanetra and Fiedler, unpublished data), and more examples still await discovery, especially in dry tropical regions.

In butterfly species with an obligate and specific association with ants, certain factors may lead to shifts to novel host ants. Like switches to novel hostplants, such shifts to new host ants could be facilitated in isolated butterfly populations[89], for example if the usual host ant becomes scarce. In fact, regional differences in host-ant relationships ('host-ant races') have been documented in a couple of lycaenid species with fragmented populations[28,69]. This suggests that adaptations in the communication signals to new host ants do occur in the 'micro-evolution' of lycaenid butterflies and may be an important selective mechanism in the evolution, and eventually speciation, among obligate myrmecophiles.

As far as their life cycles are known, however, the majority of Lycaenidae species are facultative myrmecophiles or myrmecoxenes[35]. Among these, interactions with ants are less likely to play an important role during the process of speciation[38]. Nevertheless, there are at least two ways in which myrmecophily may foster diversity even in this group of species. Ants protect lycaenid caterpillars against parasitoids and predators[93,95], and as a consequence populations of myrmecophilous lycaenids may be better buffered against the large-scale fluctuations in population size so commonly observed in the herbivorous Lepidoptera[99]. In this respect, small isolated colonies or founder populations of myrmecophilous lycaenids may survive better than non-myrmecophilous species, and this could ultimately lead to further speciation.

In addition, different ways of communicating with ants facilitates the use of the same hostplant resources. For example, on the Oriental legume tree *Saraca thaipingensis* with its associated set of ten lycaenid species, direct competition for food is weakened since most of these species differ in their particular ways of interacting with ants[108].

We hope we have demonstrated that communication between Lycaenidae butterflies and ants is not only a fascinating phenomenon from the physiologist's or behavioural ecologist's point of view, but its consequences extend far into community ecology and phylogeny.

Acknowledgements. Much of the field work underlying this study was made possible by grants from the Deutsche Forschungsgemeinschaft (Fi 547/1-1, 1-2, and the Leibniz Prize to B.H.). We thank A. Gerber for assistance with the SEM.

1 Ackery, P. R., Biocontrol potential of African lycaenid butterflies entomophagous on Homoptera. J. Afr. Zool. *104* (1990) 581-591.

2 Agosti, D., Revision of the Oriental ant genus *Cladomyrma*, with an outline of the higher classification of the Formicinae (Hymenoptera: Formicidae). Syst. Ent. *16* (1991) 293-310.

3 Atsatt, P. R., Lycaenid butterflies and ants: selection for enemy-free space. Am. Nat. *118* (1981) 638-654.

4 Atsatt, P. R., Ant-dependent food plant selection of the mistletoe butterfly *Ogyris amaryllis* (Lycaenidae). Oecologia *48* (1981) 60-63.

5 Ballmer, G. R., and Pratt G. F., Quantification of ant attendance (myrmecophily) of lycaenid larvae. J. Res. Lepid. *30* (1992) 95-112.

6 Baylis, M., and Pierce, N. E., The effects of ant mutualism on the foraging and diet of lycaenid caterpillars, in: Caterpillars – ecological and evolutionary constraints on foraging, pp. 404-421. Eds. N. E. Stamp and T. M. Casey. Chapman and Hall, New York/London 1993.

7 Burghardt, F., Untersuchungen zum Einfluß der Futterqualität auf die Myrmekophilie von Bläulingsraupen. Diplom thesis, University of Würzburg, 1994.

8 Callaghan, C. J., Notes on the biology of a myrmecophilous African lycaenid, *Aphnaeus adamsi* Stempffer (Lepidoptera, Lycaenidae). Bull. Soc. ent. Fr. *97* (1993) 339-342.

9 Cammaerts, R., Stimuli inducing the regurgitation of the workers of *Lasius flavus* (Formicidae) upon the myrmecophilous beetle *Claviger testaceus* (Pselaphidae). Behav. Proc. *28* (1992) 81-96.

10 Cammaerts, R., and Cammaerts, M.-C., Response of the myrmecophilous beetle *Edaphopaussus favieri* (Carabidae, Paussinae) to 3-ethyl-2,5-dimethylpyrazine, the only known component of its host trail pheromone, in: Biology and evolution of social insects, pp. 211-216. Ed. J. Billen. Leuven University Press, Leuven 1992.

11 Cammaerts, R., Detrain, C., and Cammaerts, M.-C., Host trail following by the myrmecophilous beetle *Edaphopaussus favieri* (Fairmaire) (Carabidae Paussinae). Insect Soc. *37* (1990) 200-211.

12 Claassens, A. J. M., and Dickson, C. G. C., A study of the myrmecophilous behaviour of the immature stages of *Aloeides thyra* (L.) (Lep.: Lycaenidae) with special reference to the function of the retractile tubercles and with additional notes on the general biology of the species. Ent. Rec. J. Var. *89* (1977) 225-231.

13 Cottrell, C. B., Aphytophagy in butterflies: its relationship to myrmecophily. Zool. J. Linn. Soc. *79* (1984) 1-57.

14 Cottrell, C. B., The extraordinary *Liphyra* butterfly. Transv. Mus. Bull. *22* (1987) 5-12.

15 Cushman, J. H., Rashbrook, V. K., and Beattie, A. J., Assessing benefits to both participants in a lycaenid-ant association. Ecology *75* (1994) 1031-1041.

16 Dejean, A., Nkongmeneck, B., Corbara, B., and Djieto-Lordon, C., Impact des fourmis arboricoles sur une pullulation d'*Achaea catocaloides* (Lepidoptera, Noctuidae) dans des plantations de cacaoyers du Cameroun, et étude de leurs Homoptères associés. Act. Oecol. *12* (1991) 471-488.

17 DeVries, P. J., The larval ant-organs of *Thisbe irenea* (Lepidoptera: Riodinidae) and their effects upon attending ants. Zool. J. Linn. Soc. *94* (1988) 379-393.

18 DeVries, P. J., Enhancement of symbioses between butterfly caterpillars and ants by vibrational communication. Science *248* (1990) 1104-1106.

19 DeVries, P. J., Call production by myrmecophilous riodinid and lycaenid butterfly caterpillars (Lepidoptera): morphological, acoustical, functional, and evolutionary patterns. Am. Mus. Novit. *3025* (1991) 1-23.

20 DeVries, P. J., Evolutionary and ecological patterns in myrmecophilous riodinid butterflies, in: Ant-plant interactions, pp. 143-156. Eds. C. R. Huxley and D. F. Cutler. Oxford University Press, Oxford 1991.

21 DeVries, P. J., Mutualism between *Thisbe irenea* butterflies and ants, and the role of ant ecology in the evolution of larval-ant associations. Biol. J. Linn. Soc. *43* (1991) 179-195.

22 DeVries, P. J., Thomas, J. A., and Cocroft, R., A comparison of acoustical signals between *Maculinea* butterfly caterpillars and their obligate host ant species. Biol. J. Linn. Soc. *49* (1993) 229–238.

23 Downey, J. C., Thrips utilize exudations of Lycaenidae. Ent. News *76* (1965) 25–27.

24 Downey, J. C., and Allyn, A. C., Butterfly ultrastructure. 1. Sound production and associated abdominal structures in pupae of Lycaenidae and Riodinidae. Bull. Allyn Mus. *14* (1973) 1–47.

25 Downey, J. C., and Allyn, A. C., Sounds produced in pupae of Lycaenidae. Bull. Allyn Mus. *48* (1978) 1–14.

26 Ehrhardt, R., Über die Biologie und Histologie der myrmekophilen Organe von *Lycaena orion*. Ber. naturf. Ges. Freiburg *20* (1914) 90–98.

27 Elfferich, N. W., Enige opmerkingen over de biologie van *Plebejus argus* L. (Lep., Lycaenidae). Entomol. Ber. Amsterdam *25* (1965) 26–31.

28 Elmes, G. W., Thomas, J. A., Hammarsted, O., Munguira, M. L., Martin, J., and van der Made, J. G., Differences in host-ant specificity between Spanish, Dutch and Swedish populations of the endangered butterfly, *Maculinea alcon* (Denis et Schiff.) (Lepidoptera). Memorabilia Zool. *48* (1994) 55–68.

29 Elmes, G. W., Thomas, J. A., and Wardlaw, J. C., Larvae of *Maculinea rebeli*, a large-blue butterfly and their *Myrmica* host ants: wild adoption and behaviour in ant-nests. J. Zool. Lond. *223* (1991) 447–460.

30 Elmes, G. W., Wardlaw, J. C., and Thomas, J. A., Larvae of *Maculinea rebeli*, a large-blue butterfly and their *Myrmica* host ants: patterns of caterpillar growth and survival. J. Zool. Lond. *224* (1991) 79–92.

31 Farquharson, C. O., Five years' observations (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 (ed. E. B. Poulton). Trans. ent. Soc. Lond. *1921* (1922) 319–448.

32 Fiedler, K., Die Beziehungen von Bläulingspuppen (Lepidoptera: Lycaenidae) zu Ameisen (Hymenoptera: Formicidae). Nachr. ent. Ver. Apollo Frankfurt, N. F. *9* (1988) 33–58.

33 Fiedler, K., New information on the biology of *Maculinea nausithous* and *M. teleius* (Lepidoptera: Lycaenidae). Nota lepid. *12* (1990) 246–256.

34 Fiedler, K., Effects of larval diet on the myrmecophilous qualities of *Polyommatus icarus* caterpillars (Lepidoptera: Lycaenidae). Oecologia *83* (1990) 284–287.

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

36 Fiedler, K., Lycaenid butterflies and plants: is myrmecophily associated with amplified hostplant diversity? Ecol. Ent. *19* (1994) 79–82.

37 Fiedler, K., Lycaenid butterflies and plants: is myrmecophily associated with particular hostplant preferences? Ethol. Ecol. Evol. *7* (1995) 107–132.

38 Fiedler, K., Life-history patterns of myrmecophilous butterflies and other insects: their implications on tropical species diversity, in: Proceedings of the international symposium on biodiversity and systematics in tropical ecosystems, in press. Ed. H. Ulrich. Museum A. Koenig, Bonn 1995.

39 Fiedler, K., and Hagemann, D. The influence of larval age and ant number on myrmecophilous interactions of the African Grass Blue butterfly, *Zizeeria knysna* (Lepidoptera: Lycaenidae). J. Res. Lepid. *31* (1995) in press.

40 Fiedler, K., and Hölldobler, B., Ants and *Polyommatus icarus* immatures (Lycaenidae) – sex-related developmental benefits and costs of ant attendance. Oecologia *91* (1992) 468–473.

41 Fiedler, K., and Maschwitz, U., Functional analysis of the myrmecophilous relationships between ants (Hymenoptera: Formicidae) and lycaenids (Lepidoptera: Lycaenidae). II. Lycaenid larvae as trophobiotic partners of ants – a quantitative approach. Oecologia *75* (1988) 204–206.

42 Fiedler, K., and Maschwitz, U., Functional analysis of the myrmecophilous relationships between ants (Hymenoptera: Formicidae) and lycaenids (Lepidoptera: Lycaenidae). III. New aspects of the function of the retractile tentacular organs of lycaenid larvae. Zool. Beitr. Berlin, N. F. *31* (1988) 409–416.

43 Fiedler, K., and Maschwitz, U., Functional analysis of the myrmecophilous relationships between ants (Hymenoptera: Formicidae) and lycaenids (Lepidoptera: Lycaenidae). I. Release of food recruitment in ants by lycaenid larvae and pupae. Ethology *80* (1989) 71–80.

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

45 Fiedler, K., and Maschwitz, U., Adult myrmecophily in butterflies: the role of the ant *Anoplolepis longipes* in the feeding and oviposition behaviour of *Allotinus unicolor*. Tyô to Ga *40* (1989) 241–251.

46 Fiedler, K., and Saam, C., Does ant-attendance influence development in 5 European Lycaenidae butterfly species? (Lepidoptera). Nota lepid. *17* (1994) 5–24.

47 Fiedler, K., Schurian, K. G., and Hahn, M. The life-history and myrmecophily of *Polyommatus candalus* (Herrich-Schäffer) from Turkey (Lep., Lycaenidae). Linneana Belg. *14* (1994) 315–332.

48 Fiedler, K., Seufert, P., Pierce, N. E., Pearson, J. G., and Baumgarten, H.-T., Exploitation of lycaenid-ant mutualisms by braconid parasitoids. J. Res. Lepid. (in press).

49 Gilbert, L. E., Adult resources in butterflies: African lycaenid *Megalopalpus* feeds on larval nectary. Biotropica *8* (1976) 282–283.

50 Henning, S. F., Biological groups within the Lycaenidae (Lepidoptera). J. Entomol. Soc. Sth. Afr. *46* (1983) 65–85.

51 Henning, S. F., Chemical communication between lycaenid larvae (Lepidoptera: Lycaenidae) and ants (Hymenoptera: Formicidae). J. entomol. Soc. sth. Afr. *46* (1983) 341–366.

52 Heppner, J. B., Faunal regions and the diversity of Lepidoptera. Trop. Lepid. *2*, Suppl. *1* (1991) 1–85.

53 Hill, C. J., The myrmecophilous organs of *Arhopala madytus* Fruhstorfer (Lepidoptera: Lycaenidae). J. Aust. entomol. Soc. *32* (1993) 283–288.

54 Hinton, H. E., Myrmecophilous Lycaenidae and other Lepidoptera–a summary. Proc. Trans. sth. Lond. entomol. nat. Hist. Soc. *1949–50* (1951) 111–175.

55 Hochberg, M. E., Clarke, R. T., Elmes, G. W., and Thomas, J. A., Population dynamic consequences of direct and indirect interactions involving a large blue butterfly and its plant and red ant hosts. J. Anim. Ecol. *63* (1994) 375–391.

56 Hochberg, M., Thomas, J. A., and Elmes, G. W., A modelling study of the population dynamics of a large blue butterfly, *Maculinea rebeli*, a parasite of red ant nests. J. Anim. Ecol. *61* (1992) 397–409.

57 Hölldobler, B., Zur Physiologie der Gast-Wirt-Beziehungen (Myrmecophilie) bei Ameisen. I. Das Gastverhältnis der *Atemeles-* und *Lomechusa*-Larven (Col. Staphylinidae) zu *Formica* (Hym. Formicidae). Z. vergl. Physiol. *56* (1967) 1–21.

58 Hölldobler, B., Orientierungsmechanismen des Ameisengastes *Atemeles* (Coleoptera, Staphylinidae) bei der Wirtssuche. Zool. Anz. Suppl. *33* (1969) 580–585.

59 Hölldobler, B., Host finding by odor in the myrmecophilic beetle *Atemeles pubicollis* Bris. (Staphylinidae). Science *166* (1969) 757–758.

60 Hölldobler, B., Zur Physiologie der Gast-Wirt-Beziehungen (Myrmecophilie) bei Ameisen. II. Das Gastverhältnis des imaginalen *Atemeles pubicollis* Bris. (Col. Staphylinidae) zu *Myrmica* und *Formica* (Hym. Formicidae). Z. vergl. Physiol. *66* (1970) 215–250.

61 Hölldobler, B., Communication between ants and their guests. Scient. Am. *1971* (March) (1971) 86–93.

62 Hölldobler, B., and Wilson, E. O., The ants. Harvard University Press 1990.

63 Howard, R. W., Akre, R. D., and Garnett, W. B., Chemical mimicry in an obligate predator of carpenter ants (Hymenoptera: Formicidae). Ann. ent. Soc. Am. *83* (1990) 607–616.

64 Howard, R. W., Stanley-Samuelson, D. W., and Akre, R. D., Biosynthesis and chemical mimicry of cuticular hydrocarbons from the obligate predator, *Microdon albicomatus* Novak (Diptera: Syrphidae) and its ant prey, *Myrmica incompleta* Provancher (Hymenoptera: Formicidae). J. Kansas ent. Soc. *63* (1990) 437–443.

65 Hummel, V., Untersuchungen zum Einfluß der Dauer einer Ameisenassoziation auf die Sekretabgabe und andere Myrmekophilieparameter der Raupen des Bläulings *Aricia agestis* (Lepidoptera: Lycaenidae). Diplom thesis, University of Würzburg, 1994.

66 Ito, F., and Higashi, S., Variance of ant effects on the different life forms of moth caterpillars. J. Anim. Ecol. *60* (1991) 327–334.

67 Jackson, T. H. E., The early stages of some African Lycaenidae (Lepidoptera), with an account of their larval habits. Trans. R. ent. Soc. Lond. *86* (1937) 201–238.

68 Jones, R. E., Ants, parasitoids, and the cabbage butterfly *Pieris rapae*. J. Anim. Ecol. *56* (1987) 739–749.

69 Jordano, D., and Thomas, C. D., Specificity of an ant-lycaenid interaction. Oecologia *91* (1992) 431–438.

70 Jutzeler, D., Weibchen der Bläulingsart *Lycaeides idas* L. riechen ihre Wirtsameisen (Lepidoptera: Lycaenidae). Mitt. ent. Ges. Basel, N. F. *39* (1989): 95–118.

71 Jutzeler, D., Kann das Weibchen von *Plebejus argus* (Linnaeus, 1761) Ameisen riechen? (Lepidoptera: Lycaenidae). Mitt. ent. Ges. Basel, N. F. *39* (1989) 150–159.

72 Kistner, D. H., The social insects' bestiary, in: Social insects, vol. 3, pp. 1–244. Ed. H. R. Hermann. Academic Press, New York 1982.

73 Kitching, R. L., and Luke, B., The myrmecophilous organs of the larvae of some British Lycaenidae (Lepidoptera): a comparative study. J. nat. Hist. *19* (1985) 259–276.

74 Laine, K., and Niemelä, P., The influence of ants on the survival of mountain birches during an *Oporinia autumnata* (Lep., Geometridae) outbreak. Oecologia *47* (1980) 39–42.

75 Lamborn, W. A., On the relationship between certain West African insects, especially ants, Lycaenidae and Homoptera. Trans. ent. Soc. Lond. *1913* (1914) 436–524.

76 Larsen, T. B., and Pittaway, A. R., Notes on the ecology, biology and taxonomy of *Apharitis acamas* (Klug) (Lepidoptera: Lycaenidae). Ent. Gaz. *33* (1982) 163–168.

77 Leimar, O., and Axén, A., Strategic behaviour in an interspecific mutualism: interactions between lycaenid larvae and ants. Anim. Behav. *46* (1993) 1177–1182.

78 Mahdi, T., and Whittaker, J. B., Do birch trees (*Betula pendula*) grow better if foraged by wood ants? J. Anim. Ecol. *62* (1993) 101–116.

79 Malicky, H., Versuch einer Analyse der ökologischen Beziehungen zwischen Lycaeniden (Lepidoptera) und Formiciden (Hymenoptera). Tijdschr. Ent. *112* (1969) 213–298.

80 Malicky, H., Unterschiede im Angriffsverhalten von *Formica*-Arten (Hymenoptera; Formicidae) gegenüber Lycaenidenraupen (Lepidoptera). Insect Soc. *17* (1970) 121–124.

81 Maschwitz, U., Fiala, B., Moog, J. and Saw, L. G., Two new myrmecophytic associations from the Malay Peninsula: ants of the genus *Cladomyrma* (Formicidae, Camponotinae) as partners of *Saraca thaipingensis* (Caesalpiniaceae) and *Crypteronia griffithii* (Crypteroniaceae). 1. Colony foundation and acquisition of trophobionts. Insect Soc. *38* (1991) 27–35.

82 Maschwitz, U., Nässig, W. A., Dumpert, K., and Fiedler, K., Larval carnivory and myrmecoxeny, and imaginal myrmecophily in miletine lycaenids (Lepidoptera: Lycaenidae) on the Malay Peninsula. Tyô to Ga *39* (1988) 167–181.

83 Maschwitz, U., Schroth, M., Hänel, H., and Tho, Y. P., Aspects of the larval biology of myrmecophilous lycaenids from West Malaysia. Nachr. ent. Ver. Apollo Frankfurt, N. F. *6* (1985) 181–200.

84 Maschwitz, U., Wüst, M., and Schurian, K., Bläulingsraupen als Zuckerlieferanten für Ameisen. Oecologia *18* (1975) 17–21.

85 Mathews, J. N. A., Aggregation and mutualism in insect herbivores. Dissertation, University of Oxford, 1993.

86 Nash, D. R., Cost-benefit analysis of a mutualism between lycaenid butterflies and ants. Dissertation, University of Oxford, 1989.

87 Peterson, M. A., The nature of ant attendance and the survival of larval *Icaricia acmon* (Lycaenidae). J. Lepid. Soc. *47* (1993) 8–16.

88 Pierce, N. E., The ecology and evolution of symbioses between lycaenid butterflies and ants. Dissertation, Harvard University, Cambridge/Massachusetts, 1983.

89 Pierce, N. E., Amplified species diversity: a case study of an Australian lycaenid butterfly and its attendant ants, in: The biology of butterflies, pp. 197–200. Eds. R. I. Vane-Wright and P. R. Ackery. Academic Press, London 1984.

90 Pierce, N. E., Lycaenid butterflies and ants: selection for nitrogen-fixing and other protein-rich food plants. Am. Nat. *125* (1985) 888–895.

91 Pierce, N. E., The evolution and biogeography of associations between lycaenid butterflies and ants. Oxford Surv. Evol. Biol. *4* (1987) 89–116.

92 Pierce, N. E., Butterfly-ant mutualisms, in: Towards a more exact ecology, pp. 299–324. Eds. P. J. Grubb and J. Whittaker. Blackwell Science Publishers, Oxford 1989.

93 Pierce, N. E., and Easteal, S., The selective advantage of attendant ants for the larvae of a lycaenid butterfly, *Glaucopsyche lygdamus*. J. Anim. Ecol. *55* (1986) 451–462.

94 Pierce, N. E., and Elgar, M. A., The influence of ants on host plant selection by *Jalmenus evagoras*, a myrmecophilous lycaenid butterfly. Behav. Ecol. Sociobiol. *16* (1985) 209–222.

95 Pierce, N. E., and Mead, P. S., Parasitoids as selective agents in the symbiosis between lycaenid butterfly larvae and ants. Science *112* (1981) 1185–1187.

96 Pierce, N. E., and Young, W. R., Lycaenid butterflies and ants: two-species stable equilibria in mutualistic, commensal, and parasitic interactions. Am. Nat. *128* (1986) 216–227.

97 Pierce, N. E., Kitching, R. L., Buckley, R. C., Taylor, M. F. J., and Benbow, K. F., The costs and benefits of cooperation between the Australian lycaenid butterfly, *Jalmenus evagoras*, and its attendant ants. Behav. Ecol. Sociobiol. *21* (1987) 237–248.

98 Pierce, N. E., Nash, D. R., Baylis, M., and Carper, E. R., Variation in the attractiveness of lycaenid butterfly larvae to ants, in: Ant-plant interactions, pp. 131–142. Eds. C. R. Huxley and D. F. Cutler. Oxford University Press, Oxford 1991.

99 Pollard, E., and Yates, T. J., Monitoring butterflies for ecology and conservation. Chapman and Hall, London 1993.

100 Quinet, Y., and Pasteels, J. M., Trail following and stowaway behaviour of the myrmecophilous staphylinid beetle, *Homoeusa acuminata*, during foraging trips of its host *Lasius fuliginosus* (Hymenoptera: Formicidae). Insect Soc. *42* (1995) 31–44.

101 Risch, S. J., and Carroll, C. R., Effect of a keystone predaceous ant, *Solenopsis geminata*, on arthropods in a tropical agroecosystem. Ecology *63* (1982) 1979–1983.

102 Rojo de la Paz, A., Two new cases of myrmecophily in the Lycaenidae (Lepidoptera): biology of *Cigaritis zohra* (Donzel, 1847) and *Cigaritis allardi* (Oberthür, 1909) in Morocco. Nota lepid., Suppl. *4* (1992) 14–17.

103 Samson, P. R., and O'Brien, C. F., Predation on *Ogyris genoveva* (Lepidoptera: Lycaenidae) by meat ants. Aust. ent. Mag. *8* (1981) 21.

104 Sanders, C. J., and Pang, A., Carpenter ants as predators of spruce budworm in the boreal forest of northwestern Ontario. Can. Ent. *124* (1992) 1093–1100.

105 Scheper, M., van der Made, J., and Wynhoff, I., *Maculinea alcon*: interactions between a myrmecophilous butterfly, its larval foodplant and its host ants. Proc. expl appl. Ent. *5* (1995) in press.

106 Schroth, M., and Maschwitz, U., Zur Larvalbiologie und Wirtsfindung von *Maculinea teleius* (Lepidoptera: Lycaenidae), einem Parasiten von *Myrmica laevinodis* (Hymenoptera: Formicidae). Ent. Gener. *9* (1984) 225–230.

107 Schurian, K. G., Fiedler, K., and Maschwitz, U., Parasitoids exploit secretions of myrmecophilous lycaenid butterfly caterpillars (Lycaenidae). J. Lepid. Soc. *47* (1993) 150–154.

108 Seufert, P., and Fiedler, K., *Drupadia ravindra* and *D. theda* (Lepidoptera: Lycaenidae): contrasting systems of myrmecophily among two closely related butterfly species, in: Les insectes sociaux, p. 275. Eds. A. Lenoir, G. Arnold and M. Lepage. Université Paris Nord, Paris 1994.

109 Shields, O., World numbers of butterflies. J. Lepid. Soc. *43* (1989) 178–183.

110 Smiley, J. T., Atsatt, P. R., and Pierce, N. E., Local distribution of the lycaenid butterfly, *Jalmenus evagoras*, in response to host ants and plants. Oecologia *76* (1988) 416–422.

111 Tautz, J., and Fiedler, K., Mechanoreceptive properties of caterpillar hairs involved in mediation of butterfly-ant symbioses. Naturwissenschaften *79* (1992) 561–563.

112 Thomas, J. A., The behaviour and habitat requirements of *Maculinea nausithous* (the Dusky Large Blue Butterfly) and *M. teleius* (the Scarce Large Blue) in France. Biol. Conserv. *28* (1984) 325–347.

113 Thomas, J. A., Elmes, G. W., and Wardlaw, J. C., Contest competition among *Maculinea rebeli* butterfly larvae in ant nests. Ecol. Ent. *18* (1993) 73–76.

114 Thomas, J. A., Elmes, G. W., Wardlaw, J. C., and Woyciechowski, M., Host specificity among *Maculinea* butterflies in *Myrmica* ant nests. Oecologia *79* (1989) 452–457.

115 Thomas, J. A., and Wardlaw, J. C., The effect of queen ants on the survival of *Maculinea arion* larvae in *Myrmica* ant nests. Oecologia *85* (1990) 87–91.

116 Thomas, J. A., and Wardlaw, J. C., The capacity of a *Myrmica* ant nest to support a predacious species of *Maculinea* butterfly. Oecologia *91* (1992) 101–109.

117 Vander Meer, R. K., and Wojcik, D. P., Chemical mimicry in the myrmecophilous beetle *Myrmecaphodius excavaticollis*. Science *218* (1982) 806–808.

118 Vane-Wright, R. I., Ecological and behavioural origins of diversity in butterflies, in: The diversity of insect faunas: pp. 56–70. Eds. L. A. Mound and N. Waloff. Academic Press, London 1978.

119 Viehmeyer, H., A myrmecophilous lycaenid chrysalis from the Philippines. Philipp. J. Sci. D *5* (1910) 73–77.

120 Wagner, D., Species-specific effects of tending ants on the development of lycaenid butterfly larvae. Oecologia *96* (1993) 276–281.

121 Wagner, D., Species-specific effects of tending ants on the life history of *Hemiargus isola*, a North American lycaenid butterfly. Dissertation, Princeton University, 1994.

122 Warnecke, G., Übersicht über die bisher als myrmekophil bekannt gewordenen paläarktischen Schmetterlingsraupen der Familie Lycaenidae. Int. ent. Z. Guben *26* (1932) 165–171, 215–219, 238–242, 285–291, 375–378, 431–433, 460–462, 479–480, 514–516; *27* (1933) 44–46, 121–127, 178–180, 305–309.

123 Warrington, S., and Whittaker, J. B., An experimental field study of different levels of insect herbivory induced by *Formica rufa* predation on sycamore (*Acer pseudoplatanus*) I. Lepidoptera larvae. J. Anim. Ecol. *22* (1985) 775–785.

124 Watkins, J. F., Gehlbach, F. R., and Baldridge, R. S., Ability of the blind snake, *Leptotyphlops dulcis*, to follow pheromone trails of army ants, *Neivamyrmex nigrescens* and *N. opacithorax*. Sthwest. Nat. *12* (1967) 455–462.

125 Wilson, E. O., The insect societies. Harvard University Press, Cambridge/ Massachusetts 1971.

126 Woodman, R. L., and Price, P. W., Differential larval predation by ants can influence willow sawfly community structure. Ecology *73* (1992) 1028–1037.