THE ECOLOGY AND EVOLUTION OF ANT ASSOCIATION IN THE LYCAENIDAE (LEPIDOPTERA)

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■ **Abstract**   The estimated 6000 species of Lycaenidae account for about one third of all Papilionoidea. The majority of lycaenids have associations with ants that can be facultative or obligate and range from mutualism to parasitism. Lycaenid larvae and pupae employ complex chemical and acoustical signals to manipulate ants. Cost/benefit analyses have demonstrated multiple trade-offs involved in myrmecophily. Both demographic and phylogenetic evidence indicate that ant association has shaped the evolution of obligately associated groups. Parasitism typically arises from mutualism with ants, and entomophagous species are disproportionately common in the Lycaenidae compared with other Lepidoptera. Obligate associations are more common in the Southern Hemisphere, in part because highly ant-associated lineages make up a larger proportion of the fauna in these regions. Further research on phylogeny and natural history, particularly of the Neotropical fauna, will be necessary to understand the role ant association has played in the evolution of the Lycaenidae.

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INTRODUCTION

The estimated 6000 species of Lycaenidae account for about one third of all
Papilionoidea (1, 55, 208, 226). Full or partial life histories have been recorded
for about 20% of these species, and of those whose full life histories are known,
about 75% [(N = 665 (Table 1)] associate with ants (95, 139, 181). These associa-
tions can be mutualistic or parasitic and range from loose facultative interactions in
which larvae are only occasionally tended by several species of ants (about 45% of
associations), to complex obligate associations in which larvae are always tended
by ants, often by only a single species (30%) (Table 1). Even when lycaenids
are not myrmecophilous, they may be protected against ant aggression by a suite
of ant-associated adaptations. The Lycaenidae are additionally characterized by
striking life history diversity. Herbivorous species consume an unusually wide
array of different plant families (10, 80), and a small number of lycaenids ($\sim$3%
of all associations or 12% of obligate ant associations) are parasitic or predatory
(48, 183).

    The behavioral and ecological diversity of the Lycaenidae makes this group par-
ticularly amenable to comparative studies of life history evolution. Colonel John
N. Eliot laid the groundwork for such research in 1973 by providing what he des-
cribed as a "tentative arrangement" of the higher classification of the Lycaenidae
(83). He later revised this scheme to comprise the five subfamilies we recog-
nize in our treatment here: the Riodininae, Curetinae, Poritiinae, Miletinae, and
Lycaeninae (44, 84; Figure 1). A molecular study by Campbell and colleagues
(35) corroborated the broad outlines of Eliot's hypothesis. The Riodininae form a
monophyletic group and are sometimes considered a separate family (124); they
are the sister taxon to the remaining four subfamilies, which together are mono-
phyletic relative to outgroups from the Nymphalidae (35). For convenience, we
refer to the latter collectively as Lycaenidae *sensu stricto* (s.s.).

Variation in Lycaenid-Ant Associations: Definition of Terms

Various workers (77, 95, 104, 139, 153, 154, 181) have categorized the degree of
lycaenid-ant associations into three broad types: obligate, facultative, and non-
ant associated. Gray areas between these categories occur, and interpretations
of facultative and obligate have varied. For clarity, we define these interactions

TABLE 1   The number and proportion (in parentheses) of ant-associated species within each lycaenid taxonomic group (subfamilies and tribes)

Taxonomic group	N	Ant-association (%)		
		Obligate	Facultative	None
PORITIINAE	44	0	0	44 (100)
Poritiini	1	0	0	1 (100)
Pentilini	11	0	0	11 (100)
Liptenini	32	0	0	32 (100)
MILETINAE	27	14 (52)	0	13 (48)
Liphyrini	5	4 (80)	0	1 (20)
Miletini	9	4 (44)	0	5 (56)
Spalgini	4	0	0	4 (100)
Lachnocnemini	9	6 (67)	0	3 (33)
CURETINAE	6	0	1 (17)	5 (83)
LYCAENINAE	588	183 (31)	299 (51)	106 (18)
Theclini	226	56 (25)	117 (52)	53 (23)
Aphnaeini	95	92 (97)	3 (3)	0
Lycaenini	36	0	5 (14)	31 (86)
Polyommatini	231	35 (15)	174 (75)	22 (10)
Total	665	197 (30)	300 (45)	168 (25)

Records compiled primarily from (17, 21, 22, 24, 39, 41, 43, 44, 48, 53, 70, 74, 77, 79, 89, 91, 93, 95, 115, 118, 125–131, 135–137, 139, 144–146, 150, 153, 155, 157–159, 163, 164, 173, 183, 190, 195, 199, 203, 205, 236, 238), and numerous journal articles of single taxa. Doubtful and hypothetical records such as predictions based on associations of closely related species are excluded, and information for Riodininae are not included (see text).

as follows and use the term entomophagy to describe the feeding behaviors of obligate parasites:

Obligate ant associations are those in which immatures are invariably associated with ants during at least some portion of the life cycle and are dependent on ants for survival under field conditions. These include both mutualistic and parasitic species. Obligate interactions exhibit considerable specificity and typically involve only a single species or genus of ant.

Facultative associations are those in which lycaenid larvae are found only intermittently associated with ants, either spatially or temporally, and do not require attendant ants for survival under field conditions. Associations are nonspecific: Larvae of a particular lycaenid may associate with ants from numerous species, genera, or even subfamilies. Most facultative associations appear mutualistic, with each partner benefiting from the presence of the other. However, a few species are facultatively predaceous, occasionally consuming the ants that normally tend them (e.g., 130).
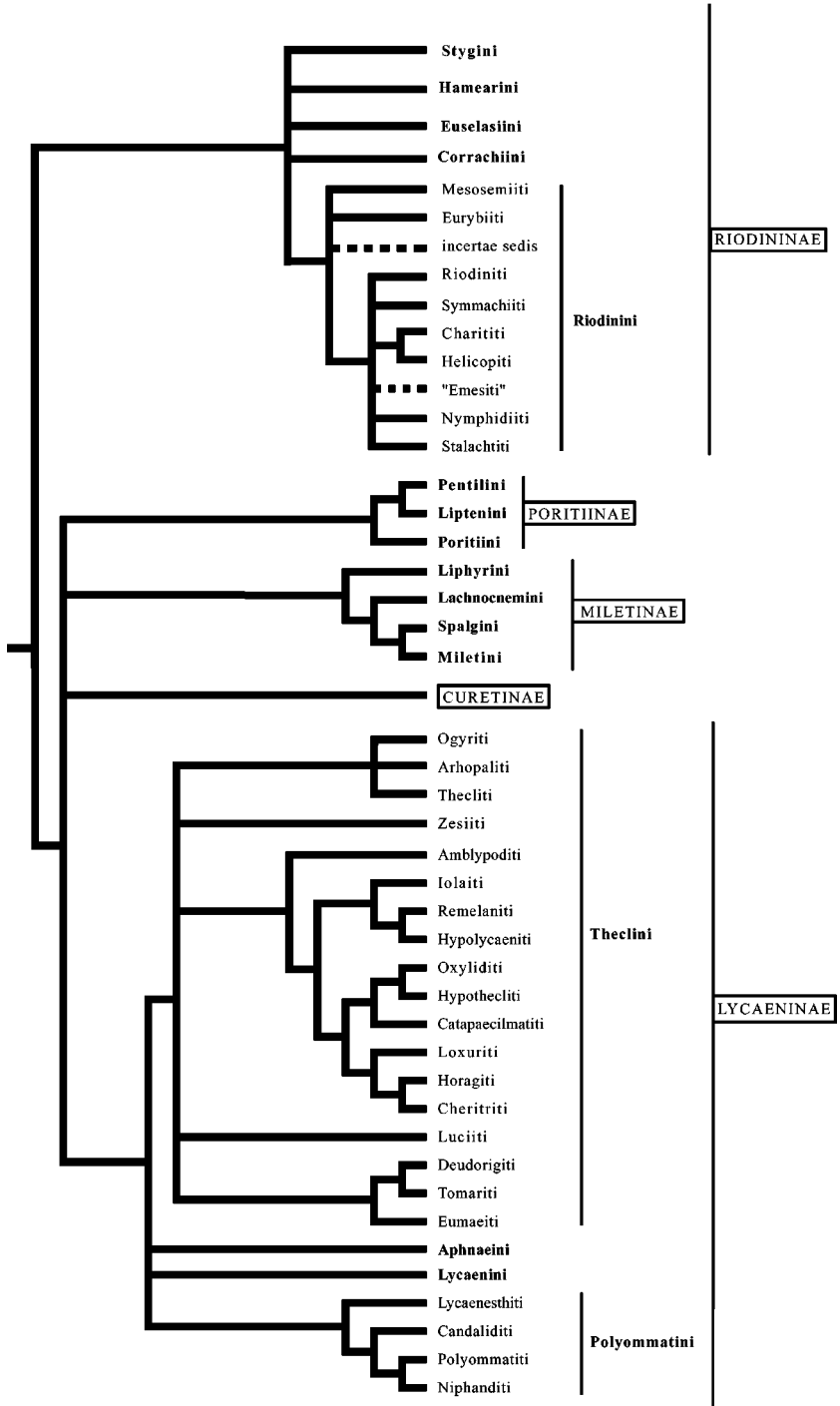
Non-ant-associated, or mymecoxenous, lycaenids are characterized by the absence of apparent associations with ants. The term myrmecoxenous underscores the notion that, unlike most lepidopterans, larvae of these lycaenids possess ant-related adaptations that protect them against aggression, even if they are not actively tended. Kitching & Luke (153) coined the term to describe species lacking a specific ant-associated organ, the dorsal nectary organ (see below), but we use it in a broader sense to describe lycaenids not tended by ants. Chemical defense from exocrine glands, hairiness, thickness of larval cuticle, and/or construction of silken shelters are some of the adaptations that protect lycaenid larvae against ants.

Entomophagy

Like other Lepidoptera, the great majority of lycaenid larvae feed exclusively on living plant tissue. However, some use insect-derived food resources during all or part of their development. These include (*a*) ant eggs, larvae and pupae (myrmecophagy), (*b*) ant regurgitations (trophallaxis), (*c*) Homoptera (homopterophagy), (*d*) homopteran honeydew, and (*e*) other lycaenid larvae (facultative cannibalism or predation).

These feeding modes have been categorized as aphytophagy, but this term can be too general when applied to species that supplement an otherwise phytophagous diet with a nonplant resource or that switch from phytophagy to aphytophagy between instars. Carnivory is likewise a limited descriptor, as it excludes food sources such as regurgitations from trophallaxis and homopteran honeydew. We instead use the term entomophagous for any species that depends on some insect-derived resource other than plant tissue at some point during its larval phase.

MECHANISMS OF INTERACTION

Ant association has exerted strong selection on lycaenid larval morphology. Presumably as a defense against ant bites, the cuticle of lycaenid larvae can be up to 20 times thicker than that of larvae from other lepidopteran families, and the head can be retracted under a sclerotized prothoracic plate (164, 165). Lycaenid larvae also have a much reduced thrashing response in the presence of ants (164, 165). This typical lepidopteran reflex may ward off some predators, but it can sometimes provoke the attention and aggression of ants (240).

DeVries (59) called the strategic deployment of ant-associated organs "enticement and binding," arguing that particular organs have specific roles in establishing

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Figure 1 Phylogeny of the Lycaenidae as proposed by Eliot (83), modified in accordance with Eliot's subsequent taxonomic revisions (44), and including Harvey's treatment of the Riodininae (taxonomic ranks adjusted; dashed lines indicate groups not thought to be monophyletic) (124) with modification from Penz & DeVries (177).

and maintaining ant associations. Most of these adaptations are found in larvae and pupae, but adults also engage in complex interactions with ants. Lycaenids manipulate ant behavior in at least three ways: suppression of ant aggression, maintenance of a "standing guard," and ant-mediated defensive measures. In addition to more general adaptations, lycaenids possess two highly specialized sets of organs used in interactions with ants: those involved in chemical mediation and those involved in acoustical mediation. For simplicity, we discuss each of these separately, recognizing that they typically function in concert with each other.

Chemical Signaling

ANT-ASSOCIATED ORGANS

Pore cupola organs   Single-celled epidermal glands called pore cupola organs (PCOs) are found on the larvae of every lycaenid species yet examined, except possibly the bizarre myrmecophage *Liphyra brassolis* (95). Although PCOs superficially resemble the much smaller lenticles found on some hesperiid caterpillars (116), there is little evidence of structural or functional homology. Lycaenid PCOs may secrete substances to pacify ants that might otherwise attack the soft-bodied larvae (113, 139, 164, 165). The PCOs may thus represent a key innovation that enabled ancestral lycaenids to benefit from enemy-free space in the presence of ants (10), with ant appeasement ultimately giving rise to more sophisticated mutualisms (61).

Tentacle organs   In the Lycaeninae, an eversible pair of tentacle organs (TOs) on the eighth abdominal segment secretes volatile substances that attract and alert ants if a caterpillar is alarmed (11, 38, 95, 106, 132). These organs are also found in the Curetinae where they are enlarged, occur more centrally on the dorsum, and may confer mechanical defense (56). In the Miletinae, only species in the genus *Aslauga* possess TOs.

Dorsal nectary organ   Restricted to species in the Lycaeninae, the dorsal nectary organ (DNO) on the seventh abdominal segment produces nutritious secretions for ants and plays a critical role in the maintenance of ant/lycaenid mutualisms (11, 160, 174). It has been called the honeydew gland by analogy with the excrement of homopterans, but it is in fact a specialized exocrine gland (165).

Apparent losses of TOs and the DNO are found throughout the Lycaenidae and are often correlated with reduced ant association. For example, larvae in the entomophagous subfamily Miletinae lack a DNO, and all but those in the genus *Aslauga* lack TOs as well. They are nonetheless ignored by the ants tending the Homoptera on which they feed, suggesting that the PCOs may appease ants in this group (48) and perhaps in the whole family.

Additional structures   Several additional structures may be important in maintaining lycaenid-ant interactions. (*a*) Dendritic setae: These erect, branched, glandular

structures are often concentrated around the DNO and spiracles (15, 17); their exact function is unknown. (*b*) Dish organs: Clark & Dickson (41) described saucer-like glands located dorsally on the fifth segment of the final instar larvae of *Spindasis* and *Crudaria* that exude a fluid the ants consume. (*c*) Perforated chambers: DeVries et al. (67) noted that the larvae of species of *Curetis* possess unusual epidermal organs of unknown function located laterally on the first thoracic segment and the seventh abdominal segment. (*d*) Papillose organs: Kitching (152) described several unusual structures on the larva of the miletine *Allotinus major* and, in particular, noted the presence of ovoid flattened organs scattered along the central axis of the larva and clustered in groups of 20 or more on lateral discs near the posterior end. Ants showed great interest in these areas, and Kitching proposed that these organs might be of special significance in the Miletinae.

Riodinine ant organs   Ant associations in the Riodininae have traditionally been described from three relatively derived ant-associated subtribes [Eurybiiti, Lemoniiti, and Nymphidiiti (63, 124)]. Recent phylogenetic work by Penz & DeVries (177), however, shows that the Lemoniiti are rooted within the Nymphidiiti, so the three groups collapse to two, the Eurybiiti and Nymphidiiti.

Nutritious droplets are secreted from paired tentacle nectary organs (TNOs) on the eighth abdominal segment, while paired anterior tentacle organs (ATOs) on the third thoracic segment presumably emit volatile compounds (63). Differences in the location and structure of ant-associated glands between riodinines and their sister taxa have been cited as evidence for convergence of both form and function (61). In view of the evolutionary importance of tagmatization in arthropods, however, and the ease of switching between segment identities, it is possible that these organs are homologous (34).

SUPPRESSION OF ANT AGGRESSION   Much discussion (48, 88, 106, 164, 182) and some data (3, 132, 134) suggest that lycaenid larvae suppress ant aggression in part by mimicking aspects of the pheromones of ant brood. Attendant ants lick and antennate lycaenid larvae much as they do their own brood. The substance(s) responsible in both cases is widely dispersed over the cuticle and relatively non-volatile, persisting for several days after death (27, 106, 113, 182, 234). The larvae of parasitic inquiline lycaenids are often deposited by workers in the brood chamber of the ant nest alongside the immature ants (217, 219).

Henning (132, 134) showed that the lycaenids *Aloeides dentatis* and *Lepido-chrysops ignota* chemically mimic the brood of their respective attending ants *Lepisiota capensis* and *Camponotus niveosetosus*. Similarly, Akino and colleagues (3) demonstrated that larvae of the lycaenid *Maculinea rebeli* produce a profile of hydrocarbon compounds sufficiently similar to that of *Myrmica schencki* ant larvae to induce *M. schencki* workers to carry *M. rebeli* larvae into their nests, where the caterpillars eat the brood. They showed that after seven days inside the nest, the lycaenids acquired several more presumably colony-specific hydrocarbons and became nearly perfect chemical mimics of the ant brood.

Some authors nevertheless doubt the existence of brood pheromones in ants (169, 224). Ants can clearly differentiate brood from workers and discriminate among different types of brood (e.g., worker-biased larvae, queen-biased larvae, worker pupae) (161). The experimental problem is to distinguish between a feeding response in which an object is carried into the brood chamber from a similar response elicited by an object coated with brood pheromone. This remains a weakness of all published studies on lycaenids (3, 132, 134). Nevertheless, recent studies (156, 221) have demonstrated that cuticular hydrocarbons communicate colony membership in worker ants, and hydrocarbons may serve a related purpose in labeling ant brood in some as-yet-unknown way.

Even if cuticular hydrocarbon matching is responsible for suppressing ant aggression toward lycaenid immatures, it remains to be seen whether PCOs are involved in their production. While PCOs are unique to lycaenid immatures, cuticular hydrocarbons are ubiquitous among insects as they serve essential roles in waterproofing and osmoregulation (120, 172).

MAINTENANCE OF A "STANDING GUARD" OF ANTS   The persistence of ants in attending caterpillars may depend on the mode of appeasing ant aggression (such as ant brood chemical mimicry) but may also relate more directly to the quantity and quality of nutritive rewards offered to ants. Lycaenids producing particularly valuable secretions would be expected to maintain a larger cadre of dominant, aggressive attending ants than those producing less valuable secretions, as seen in aphids (227).

The nutritive rewards secreted by immatures of several lycaenid species have been analyzed chemically. Maschwitz et al. (167) found carbohydrates (13–19%) and trace amounts of methionine from the DNO secretion of the facultative ant associate, *Lysandra hispana*. Pierce (182, 188) also found carbohydrates to be an important component of the DNO secretions of the Australian lycaenid, *Jalmenus evagoras*, making up about 10% dry weight. These secretions also contained at least 14 different free amino acids, particularly serine, in concentrations ranging from 20 to 40 mM, depending on the time of day (188). DeVries found that TNO secretions from the riodinine *Thisbe irenea* contain at least 18 amino acids, with glutamine and glycine predominating, and small amounts of sugars (<0.5%) (57, 64).

Behavioral assays indicate that host plant quality can affect the secretions from lycaenid larvae (19, 94). Baylis & Pierce (19) applied fertilizer to alter the quality of the foliage of seedlings of *Acacia decurrens*. Late instar larvae of *J. evagoras* reared on high-quality host plants were tended by more ants and had higher survivorship in the field than counterparts feeding on low-quality unfertilized plants, and females also preferred to lay eggs on these high-quality plants.

Lycaenid larvae can manipulate their attendant ants by strategically varying the rate at which they provide rewards in a manner similar to the production of inducible defenses in plants (2). When under a perceived threat (a pinch from forceps),

larvae of both *Polyommatus icarus* (160) and *Plebejus acmon* (2) secrete more rewards and/or attractants from the DNO and thereby attract a greater number of attendant ants. Individual larvae of *J. evagoras* also regulate secretions depending on social context: Larvae in a group of five secrete significantly less per capita than each does when alone (12). Beyond a threshold number of ant guards, the benefit from producing metabolically expensive secretions may have diminishing returns (11, 160).

Wada and colleagues (228) found that the DNO secretions of the parasitic larvae of *Niphanda fusca* fed by worker trophallaxis in the nest contain high titres of glucose and glycine. Recordings from the taste receptors of the attendant ant species, *Camponotus japonicus*, showed that the presence of even trace amounts of glycine when combined with glucose made these solutions much more attractive to attendant ants.

Eavesdropping on ant trail pheromones has been demonstrated in the behavior of *Euliphyra mirifica* and *Euliphyra leucyana*, which are parasites of arboreal weaver ants, *Oecophylla longinoda* (54). Adult females of a close relative, *L. brassolis*, typically lay eggs on foliage adjacent to established nests of *Oecophylla smaragdina*. The first instars probably locate the ant nests by following ant trail pheromones. Larvae must also move between nests after they have consumed the brood within a nest or whenever host ants abandon old nests and construct new ones (43).

ANT-MEDIATED DEFENSE TACTICS   Myrmecophilous lycaenid caterpillars can signal distress to their ant entourage. Larvae typically evert their TOs or ATOs, and ant behavior following this signal is similar to that released by ant alarm pheromone. Mimicry of an ant's alarm pheromone has been documented in the Australian spider *Habronestes bradleyi*, which uses the chemical to disorient its ant prey, *Iridomyrmex purpureus* (5).

Alarm pheromones are among the least species-specific class of ant pheromones, and often the same chemical provokes an alarm response in species from different subfamilies (23, 142, 175). Thus, a lycaenid that produces an ant alarm pheromone mimic might communicate the need for protection with multiple ant species. Ant alarm pheromones and TO/ATO pheromones are highly volatile, which makes pheromone collection for chemical analysis difficult. Henning (132), however, succeeded in extracting the posterior half of *Aloeides dentatis* (which contains the TOs) in dichloromethane, and these extracts elicited an alarm response from attending ants in bioassays. These ants responded similarly when presented with dichloromethane extracts from conspecific mandibular glands, which produce alarm pheromones in several ant species (25, 142).

ADULTS   Ant workers frequently do not interact with the adults of myrmecophilous Lycaenidae, or if they do, treat them much as they would any insect prey. For example, among species of *Chrysoritis* and *Thestor*, adults are killed

and eaten if they fail to escape from their corral or byre on eclosion. Species that eclose inside ant shelters are frequently cloaked in "eclosion wool," a layer of deciduous scales that slough off in an ant's mandibles and tarsi, enabling the teneral adult to slip away. Nevertheless, several observations suggest that chemical interactions between adults and ants may be more complex than currently appreciated, and some adults may appease ants that would otherwise attack them.

For example, Atsatt (10) suggested that adults of the lycaenids *Teratoneura* and *Epitolina* use pheromones to drive away attending ants from extra floral nectaries or coccids so they can feed on them themselves (91). DeVries (56) noted that workers of *Anoplolepis longipes* tending larvae of *Curetis regula* were keenly interested in the adults, palpating them with their antennae and appearing to feed near the base of the butterfly's extended proboscis. Larvae of the Australian species *Ogyris genoveva* shelter within specially constructed byres at the base of their host plants, and teneral adults harden their wings in this shelter without harassment (75). Ovipositing females of the Asian species *Anthene emolus* are initially attacked by their host ant, *Oecophylla smaragdina*, but workers cease attacking once a female has begun laying eggs perhaps because the eggs release an appeasement pheromone (109).

Ant-dependent mate selection and oviposition   Behavioral evidence indicates that ants may also be used as mating and oviposition cues. Males of the Australian species *J. evagoras* use ants as cues in finding available females (82). The females of a number of myrmecophilous lycaenids use attendant ants as oviposition cues (9, 108, 109, 132, 185, 209, 232). The great majority of these are species with obligate ant association (e.g., 185), although some are facultatively associated (232). Significantly from the point of conservation practices, experiments have failed to find ant-dependent oviposition not only among females of facultative species (184), but also among obligately associated species of *Maculinea* (217, 215). However, analyses taking into account host plant phenology, intraspecific competition in egg deposition, and location of ant nests show that ant-dependent oviposition may occur in at least one species, *Maculinea alcon*, but simply be difficult to detect experimentally (225). Differences in adoption times depending on ant hosts have been measured for caterpillars from separate populations of *M. alcon* (6), and genetically differentiated populations of this species are suggestive of host ant specialization (119).

Females from populations of *J. evagoras* show a remarkable degree of specificity in ant-dependent oviposition, preferring to lay eggs in response to cues from their natal ant population rather than other populations of ants of the same species (117). To date, no investigations have addressed the possible chemosensory significance of females tapping their antennae or dragging their ovipositors on ant-infested host plants (82, 117, 185). A number of ant-associated insects locate ants through ant trail pheromones (4, 33, 54), which the chemosensory structures in the antennae and ovipositors of adult female lycaenids may likewise be capable of detecting.

Acoustic Signaling

Most sound production in the Lepidoptera has evolved in response to selection on sexual or defensive traits (90); juvenile sound production in the Lycaenidae also mediates associations with ants.

PUPAL SOUND PRODUCTION: MECHANISMS AND DISTRIBUTION   Lycaenid pupae produce sound by a mechanism that is widespread among lepidopteran pupae: stridulation, the act of grating a file lined with teeth against a hardened plate (71). In lycaenids, the file-and-scraper organ is found in the intersegmental region between abdominal segments 4–5, 5–6, or 6–7.

Lycaenid pupae can give three distinct signals (73, 141). A primary signal, often produced by stimulation of the pupa, is detectable without amplification. A secondary signal is of lower amplitude, consisting of a set of clicks produced in bursts, sometimes interspersed between primary signals. Tertiary signals consisting of low-amplitude background clicking sounds have been detected only in the largest pupae.

A pupal stridulatory organ has been found in every lycaenid pupa examined (72, 81), including both ant-associated and non-ant-associated taxa. This includes ten species of riodinine pupa in the tribe Hamearini and five subtribes of the Riodinini. Each of these riodinine pupae possesses two sets of file-and-scraper stridulatory organs, located between abdominal segments 4–5 and 5–6.

PUPAL SOUND PRODUCTION: FUNCTION   Calls are induced when pupae are disturbed, and Downey & Allyn (73) concluded that calls act primarily as a deterrent to predators and parasites. Travassos & Pierce (222) showed that pupal calling is also involved in ant recruitment. In pairs of pupae of *J. evagoras*, where one member was experimentally muted, calling pupae attract and maintain a higher ant guard than their silent counterparts. Eastwood & King (78) observed that pupae of the myrmecophage, *Arhopala wildei*, emitted a prolonged "burr" lasting several seconds upon reintroduction to the ant nest. The pupae also oscillated with a rapid dorso-ventral movement of the anterior end in a frequency that matched the frequency with which the host ants tapped the substrate when alarmed.

DeVries (60) surveyed 26 species of pupae in the Riodininae but found no evidence of pupal sound production. However, experiments conducted by Ross (197) on *Lemonia caliginea* (=*Anatole rossi*) suggest that sound production in riodinine pupae may play a role in attracting ants. In addition to a pair of stridulatory organs, *L. caliginea* pupae possess a pair of glands on the metathoracic segment that may produce a chemical attractive to ants (196). Ross found that a fast-drying lacquer applied to either the paired metathoracic organs or the stridulatory organs, but not both, did not eliminate ant tending of the pupae. However, on occluding both sets of organs, the attendant ants abandoned the pupa after 48 h. Ross hypothesized that the stridulatory organs and metathoracic glands work in concert to attract and maintain attendant ants.

LYCAENID *SENSU STRICTO* LARVAL SOUND PRODUCTION   Lycaenids (s.s.) typically start producing calls in the third instar, when other myrmecophilous organs develop (60), although larvae of *Hemiargus isola* have been recorded to start calling in the second instar (D. Wagner, personal communication). In general, these calls resemble a slow drumming compared with the faster chirps of the riodinines. They travel primarily through the substrate, although they also have an airborne component (60, 201). DeVries (60) first noted that some lycaenid calls have two signals: a low background sound accompanied by a constant pulse. Travassos & Pierce (222) found that *J. evagoras* larvae produce three signals that differ in acoustic properties and amplitudes: the grunt, drum, and hiss.

Hill (138) localized rapid trembling to abdominal segments five and six of *Arhopala madytus* and described a file of teeth found on the posterior margin of the fifth abdominal segment that rubs against an opposing plate on the anterior margin of the sixth abdominal segment. *A. madytus* larvae thus produce calls with a stridulatory organ similar to that found in lycaenid pupae, although the position of the file and scraper are reversed. Schurian & Fiedler (202) observed that larvae in the genus *Polyommatus* use dorsal, longitudinal, and lateral muscles on abdominal segments 4–7 when producing calls.

Because the organs for sound production in lycaenids remain poorly characterized, we cannot determine how widespread they may be within the family. In his sound production survey, DeVries (59, 60) found that only myrmecophilous lycaenids produce calls, and several non-ant-associated members of the Eumaeiti are silent. However, since then, several non-myrmecophilous lycaenids have been observed to produce sound, including *Deudorix epijarbas* (52), *Caleta roxus* (100), *Caleta manovus* (100), and *Cheritra freja* (98). *Callophrys rubi*, *Curetis bulis*, and *Curetis santana* also produce sound, but accounts of whether ants attend these species conflict (26 versus 113 and 56 versus 112). Fiedler (97) suggested that the ability to produce calls may be universal in the Lycaenidae: Whereas non-ant-tended lycaenids produce simple calls in response to a disturbance, ant-tended lycaenids have calls of greater complexity that are produced more often.

DeVries (58), Fiedler (98), and D. Wagner (personal communication) observed that lycaenid larvae produce sounds when disturbed, suggesting a defensive function. DeVries (60) argued that lycaenid calls, like riodinine calls, attract ants. Travassos & Pierce (222) found that two calls produced by larvae of the lycaenid, *J. evagoras*, the grunt and hiss, are more common in the presence of attendant ants. Moreover, the calls of *Maculinea* larvae and the stridulations of the *Myrmica* ants they parasitize share the same pulse length and dominant frequency, suggesting a convergence of caterpillar calls on those produced by host ants (66). Lycaenids that form obligate associations with different ant species may have evolved different acoustic signals. Attendant ants are widely distributed phylogenetically, including representatives from the subfamilies Myrmicinae, Dolichoderinae, and Formicinae (77). Of these, only myrmicines are known to produce calls via stridulation, whereas some dolichoderine and formicine ants produce vibratory signals by drumming body parts on the substrate (142, 166).

LARVAL SOUND PRODUCTION IN RIODININAE   Riodinine larvae produce sound by different mechanisms than from those of the Lycaenidae (s.s). Some riodinine larvae have a pair of vibratory papillae on the distal edge of the prothorax, each one bearing concentric grooves along its length (62). When a caterpillar oscillates its head, epicranial granulations on the head slide across these grooves, producing low-amplitude calls that travel solely through the substrate, unlike the airborne songs of crickets. DeVries (57) compared the ant attendance levels between normal caterpillars of *T. irenea* with those that had their papillae removed and found that calling caterpillars were tended by more ants.

COSTS AND BENEFITS OF LYCAENID-ANT INTERACTIONS

Early studies of costs and benefits of lycaenid-ant interactions focused on the benefits of the lycaenids, generating two nonexclusive hypotheses. The appeasement hypothesis is simply that ant-associated lycaenid larvae (excluding those species parasitic on host ants) benefit from not being attacked by ants. The food rewards they provide attendant ants can be regarded as a kind of bribery (162, 164, 165). The protection hypothesis argues that attendant ants guard lycaenid larvae against predators and parasites, and in turn they are rewarded with nutritious secretions (212). Experimental studies have shown that ants can function as protective guards in this way, although the importance of ant protection varies among species (61, 107, 111, 184, 186, 187, 197, 198, 206, 229–231; but see 178). This does not preclude the possibility that ant-tended lycaenids also appease otherwise aggressive ants and thereby inhabit enemy-free space (10).

Attendant ants can affect lycaenid development and/or reproductive success (20, 16, 49, 82, 105, 110, 186, 192, 229, 233). In mutualistic interactions, the cost for this net benefit is sometimes meted out in terms of adult weight and size. Larvae and pupae of *J. evagoras* tended by ants are considerably (25%) lighter and smaller than experimental counterparts not tended by ants (186). Because size and weight are determinants of female fecundity and male reproductive success in *J. evagoras* (82), this size reduction represents a significant cost. Additional costs can come in the form of increased apparency: Some parasitoids use chemical cues from host ants to find their lycaenid prey (140, 213).

Other lycaenids, such as the facultative *Hemiargus isola* (229) and the obligate *Paralucia aurifera* (49), may compensate for the secretions they give up to attendant ants. *H. isola* eclose at a heavier weight when tended by one species of ant, and *P. aurifera* develop more quickly and gain more weight when tended by ants perhaps because they spend more time feeding when tended. Some species exhibit sex-specific effects during development, wherein one sex supports more of the cost of the mutualism than the other. Thus, *Polyommatus icarus* males develop relatively more quickly than their female counterparts when tended by ants (105), and males of *J. evagoras* experience relatively less reduction in size than their female counterparts when tended by ants (20).

In parasitic interactions, lycaenid larvae that enter the host ant nest during some portion of their lifetimes have unusually variable development (183). Some have prolonged developmental times, often overwintering as larvae in the nest (133), some are variable with respect to overwintering (200), and others vary considerably in final adult size (18, 78). Elmes et al. (87) showed that phytopredaceous lycaenids such as species of *Maculinea* and other parasites of ants also have unusual growth patterns between instars. The small, phytophagous early instars have regular growth, but the entomophagous final instar has >10 times the growth predicted by extrapolating from the early stages (following Dyar's rule). These growth patterns are similar to those exhibited by their *Myrmica* ant hosts.

The costs and benefits to the ants in lycaenid/ant interactions have been less well studied; it has been assumed that ants receive a net nutritional benefit from harvesting secretions despite the metabolic cost of protecting caterpillars. However, sometimes the ants do not benefit, as exhibited most dramatically by species that parasitize host ants. More subtle forms of manipulation have been demonstrated by the strategic, or inducible, nature of the rewards offered to ants by different lycaenid species (2, 12, 160). Natural selection should favor strategies whereby it is less expensive metabolically to fool ants into attendance while still receiving a net benefit.

As described above, attendant ants are rewarded with nutritious secretions (49, 57, 107, 167, 186, 230), and workers of some species live longer when allowed access to lycaenid secretions (49, 110, 111). Queenright colonies of the attendant ant *Iridomyrmex rufoniger* showed net gains in growth rate when their food was supplemented with secretions from larvae of *J. evagoras* (171, 188).

Effects of Ant Association on Host Plant Choice

Experimental cost/benefit studies of lycaenid-ant interactions have elucidated selective mechanisms promoting and maintaining associations, and these in turn have suggested potential evolutionary repercussions that might be expected among ant-associated species.

Pierce (180) investigated whether ant-associated lycaenids that reward ants with protein-rich secretions are also more likely to feed on legumes and other protein-rich–host plant species. Similarly, Pierce & Elgar (185) assessed whether lycaenids that use ants as well as plants as cues for oviposition feed on a wider range of host plant taxa than those that do not. Fiedler subsequently re-examined these and other patterns using many additional life history records (95, 99, 101–103). With a number of conditional caveats, these two patterns of host plant use appear to be supported when analyzed with larger data sets (101, 99). Leguminous–host plant use is correlated with larval ant association, and phytophagous lycaenids that obligately associate with ants use a wider range of host plants than lycaenids that do not associate with ants.

However, none of these comparative studies has taken into account phylogenetic effects, in part because of our limited knowledge of the phylogeny of

the Lycaenidae, making the validity and/or functional significance of these patterns impossible to evaluate. Additional information about the phylogeny of the Lycaenidae will be necessary to identify appropriate independent contrasts (92) to test hypotheses about the evolution of ant association and host plant use.

Ants as a Template for Butterfly Diversification

Attendant ants influence many aspects of lycaenid physiology, behavior, and ecology. In obligately mutualistic lycaenids, overlapping requirements of suitable host plants and attendant ants can lead to population fragmentation and small population sizes, thus promoting genetic divergence among populations (10, 45, 46, 114, 149, 179, 206, 209). The history of ant association may therefore be reflected in the cladogenesis of ant-associated butterflies, and at least two lines of evidence suggest that this is the case.

First, phylogenetic studies of four independent lineages of ant-associated lycaenids have shown that sister taxa typically share closely related ant associates: Taxa within the Aphnaeini, Ogyriti, Zesiiti, and Luciiti all show phylogenetic conservatism with respect to ant association. The genus *Chrysoritis* (Aphnaeini) associates largely with *Crematogaster* ants (Myrmicinae). Other aphnaeines, including species of *Phasis* and *Tylopaedia*, also associate with myrmicines. In contrast, aphnaeines in the genera *Trimenia* and *Crudaria* associate primarily with ants in the subfamily Formicinae, thereby forming distinctive clades within a largely myrmicine-associated group (191, 211).

Most strikingly, the species of the Australian genus *Ogyris* form several distinctive clades that correspond well with their ant affiliations. For example, *Ogyris genoeveva*, *Ogyris zosine*, *Ogyris idmo*, *Ogyris subterrestris*, and *Ogyris otanes* all associate with Formicinae and are each other's closest relatives; the group containing *Ogyris ianthis*, *Ogyris iphis*, and *Ogyris aenone* associates with Dolichoderinae; and the clade containing *Ogyris oroetes*, *Ogyris olane*, and *Ogyris barnardi* has lost or greatly reduced association (N.E. Pierce, A.A. Mignault, G.S. Adelson, R. Eastwood, D.J. Lohman, M. Blair & T. Itino, manuscript in preparation).

Within the Australian genus *Jalmenus*, a small group of closely related taxa (*Jalmenus eichhorni*, *Jalmenus lithochroa*, and *Jalmenus ictinus*) interact primarily with the highly distinctive *Iridomyrmex purpureus*–species group and its close relatives (77, 188, 207).

Finally, the basal members of the entomophagous Australian genus *Acrodipsas*, *A. myrmecophila* and *A. brisbanensis*, associate with ants in the Dolichoderinae. A speciation event associated with a host-ant shift to Myrmicinae occurred in the ancestor of the clade containing the sister taxa *Acrodipsas cuprea* and *Acrodipsas aurata*, which further gave rise to the five members of the *illidgei* species group. Although the host ants of four species in this group are still unknown, the larvae of *Acrodipsas illidgei* itself also feed on ants in the Mymicinae (76).

Just as shifts onto novel host plants may serve as a key adaptation that permits diversification, shifts by lycaenids to chemically and behaviorally novel clades

of ants may facilitate subsequent radiation. Note, however, that this evolutionary relationship is asymmetrical. Whereas certain lycaenids are obligate in their dependence on attendant ants, the reverse is not true; attendant ants have alternative food sources in the field. Ants may be regarded as a template against which the lycaenids have diversified but not vice versa.

A second line of evidence that ant associations may affect patterns of diversification comes from a recent study of the genitalia of ant-associated and non-ant-associated Lycaenidae. Heath (125) found a strong correlation between the degree of ant association and the uniformity of male genital features. Species in highly ant-associated genera have extremely uniform genitalia, whereas species in non-ant-associated genera have widely divergent genitalia. Explanations of this pattern include the possibility that myrmecophilous lycaenid species have diversified more recently than their less-myrmecophilous sister groups. Alternatively, adult male lycaenids may use ant associates as cues for finding mates (82), thus relaxing any potential lock-and-key selection mechanism affecting their genitalic complexity. Finally, ant cues may enable adult males of some lycaenid species to find conspecific pupae so that females are mated immediately on eclosion, thereby relaxing sexual selection via female choice (8).

ENTOMOPHAGY AND ANT ASSOCIATION

Phylogenetic Distribution

Obligate entomophagy appears throughout the entire subfamily Miletinae and in small entomophagous clades and occasional species scattered throughout the Lycaeninae and Riodininae (Table 2).

The Miletinae are entirely aphytophagous: Most species feed on Homoptera. Exceptions include the obligate myrmecophiles in *Liphyra* and *Euliphyra* (Liphyrini). *L. brassolis* has a tank-like morphology to repel ant attack and feeds on the brood of *O. smaragdina* (48, 69, 165). *E. mirifica* subsists on regurgitations from *O. longinoda* (54) and possesses a far thinner cuticle than *Liphyra*, its sister group.

The genus *Thestor* (Lachnocnemini), endemic to southern Africa, represents one of the largest radiations within the Miletinae (∼29 spp.). Some species of *Thestor* prey on coccids (40); trophallaxis and detritivory have also been recorded (130). At least three species of *Thestor* are known to associate with the formicine ant *Anoplolepis custodiens*, and it has been suspected that most are likewise affiliated with *A. custodiens*. However, it is unlikely that so many sympatric species could simultaneously parasitize the same ant, leading to the as yet untested hypothesis that *A. custodiens* consists of a constellation of sibling species.

A group that seems remarkably specific in its indirect host-ant affiliations is the Miletini. Fiedler (103, 104) proposes that species of *Miletus* and *Logania* may maintain specific associations with ants in the Dolichoderinae and feed only on

homopteran prey that are being tended by these ants. Species in the Spalgini, including *Taraka*, *Spalgis*, and *Feniseca*, likewise prey more frequently on homopterans tended by ants in the Formicinae, although this could be because Formicinae are more abundant in the habitats where these lycaenids live. Nevertheless, the ant affiliations of these two clades hint at the possibility of a "ghost of ant-association past", and it is possible that associations with specific ants may have facilitated prey location and exploitation by these groups. In contrast, other miletines feeding only on Homoptera and/or honeydew are associated with a broad taxonomic range of ants (Table 2).

Widespread entomophagy occurs in three tribes of the subfamily Lycaeninae: Aphnaeini, Theclini, and Polyommatini. Assuming the monophyly of genera (supported by molecular analysis in some cases), there have been at least 20 independent shifts away from phytophagy during the evolution of the Lycaeninae (Table 2). Most of these shifts appear either as single entomophagous species within phytophagous clades or as small entomophagous genera (5–9 spp.) representing limited radiations. The species-rich *Lepidochrysops* (126 spp.) is one major exception.

The primarily African tribe Aphnaeini exhibits several independent shifts to entomophagy. *Chrysoritis dicksoni*, alone among the numerous species of its genus, survives exclusively on trophallaxis from *Crematogaster* ants (41, 48, 126, 127, 130). There are also some older records of trophallaxis by *Axiocerces harpax* (146) and *Chloroselas pseudozeritis umbrosa* (145). Jackson (146) hypothesized that more species within *Axiocerses*, *Chloroselas*, and *Spindasis* feed via trophallaxis or detritivory, based on the relatively small larval mouthparts in these three genera. To date, however, life history studies have uncovered only one thoroughly entomophagous clade within the Aphnaeini. The genus *Trimenia* contains five species that lack DNOs in the final instar and appear to be entomophagous (41, 48, 129, 130). Heath (125) suggests that *Argyrospodes argyraspis* is sister to *Trimenia* and is likely to share similar characteristics.

Although the large (∼50 spp.) genus *Aloeides* was thought to be wholly phytophagous, recent studies point to at least one shift to entomophagy. *Aloeides pallida grandis*, which unlike many *Aloeides* species lacks a DNO in the final instar, can survive for up to four months in *Lepisiota* (Formicinae) nests without emerging to forage on host plants and can feed on ant eggs (130). A few other species of *Aloeides* also lack a final-instar DNO, as does *Phasis thero*, although entomophagy has not been directly observed in these species.

Several independent instances of entomophagy are found in different subtribes of the Theclini, and these are concentrated in Australia. *Arhopala wildei* (Arhopaliti) is the only confirmed entomophagous species in a large and widespread genus (∼120 spp.). Larvae feed on the brood of their ant attendants, *Polyrhachis queenslandica*, even as they feed the workers with DNO secretions (24, 151, 78). The closely related species *O. idmo* and *O. subterrestris* (Ogyriti) comprise another probable origin of obligate entomophagy within a smaller genus (13 spp.) (24). Finally, the Australian endemic genus *Acrodipsas* (Luciiti; 9+ spp.) represents the only limited radiation of entomophagous theclines known to date. Larvae of five

TABLE 2 Lycaenid species with entomophagous life histories (24, 48, 63, 65, 68, 76, 95, 125, 127–130, 139, 183, 190, 223)

Confirmed entomophagous species (named if <3)	Species number[a]	Food source[b]	Ant associate (genus)	Distribution
Miletinae				
Liphyrini				
Liphyra brassolis, *L. grandis*	2/2	Bro	*Oecophylla*	Australian, Oriental
Euliphyra leucyania, *E. mirifica*	2/2	Tro	*Oecophylla*	African
Aslauga (9 spp.)	20/20	Hom		African
Miletini				
Allotinus (6 spp.)	30/30	Hom	*Anoplolepis*, *Crematogaster*, *Oecophylla*, *Technomyrmex*	Oriental
Logania malayica, *L. marmorata*	10/10	Hom/Hon/Tro	*Leptothorax*	Oriental
Lontalius (0 spp.)	1/1	?		
Megalopalpus zymna	4/4	Hom	*Pheidole*	Afrotropical
Miletus (5 spp.)	20/20	Hom	*Crematogaster*, *Dolichoderus*, *Pheidole*, *Polyrhachis*	Oriental
Spalgini				
Spalgis epius, *S. lemolea*	5/5	Hom	*Crematogaster*, *Oecophylla*	African, Oriental
Taraka hamada	2/2	Hom/Hon		Palaearctic, Oriental
Feniseca tarquinius	1/1	Hom/Hon	*Camponotus*, *Formica*, *Lasius*, *Myrmica*	Nearctic
Lachnocnemini				
Lachonocnema bibulus, *L. brimo*, *L. durbani*	12/12	Hom/Hon/Bro	*Camponotus*, *Crematogaster*, *Pheidole*	African
Thestor basutus, *T. protumnus*, *T. yildizae*	27/27	Hom/Tro/Det	*Anoplolepis*	African
Lycaeninae				
Theclini				
Arhopaliti				
Arhopala wildei	1/120	Bro	*Polyrhachis*	Australian
Luciiti				
Acrodipsas aurata, *A. brisbanensis*, *A. cuprea*, *A. illidgei*, *A. myrmecophila*	9/9	Bro	*Crematogaster*, *Papyrius*	Australian
Ogyriti				
Ogyris idmo, *O. subterrestris*	2/14	Tro?	*Camponotus*	Australian

TABLE 2   (*Continued*)

Confirmed entomophagous species (named if <3)	Species number[a]	Food source[b]	Ant associate (genus)	Distribution
Thecliti				
Shirozua jonasi	1/1	Tro/Hom	*Lasius*	
Zesiiti				
Zesius chrysomallus	1/1	Phy/Bro?	*Oecophylla*	South Asian
Aphnaeini				
Aloeides pallida grandis	1/50	Eggs/Phy	*Lepisiota*	African
Aphnaeus adamsi	1/20	Tro/Fung	*Crematogaster*	African
Argyrospodes argyraspis	1/1	?	?	African
Axiocerses harpax	2/10	Tro	*Crematogaster*	African
Chloroselas pseudozeritis umbrosa	1/14	Tro?	*Crematogaster*	African
Chrysoritis dicksoni	1/58	Tro	*Crematogaster*	African
Cigaritis [*Apharitis*] *acamas*, *C.* [*Spindasis*] *nyassae*, *C.* [*Spindasis*] *takanonis*	3/65	Tro/Bro	*Crematogaster*	African, Japanese
Trimenia agyroplaga, *T. wallengrenii*, *T.* [*Argyrocupha*] *malagrida*	5/5	Tro/Bro	*Anoplolepis*	African
Polyommatini				
Lycaenesthiti				
Anthene levis	1/90	Tro	?	
Triclema lamias	1/20	Hom	?	African
Niphanditi				
Niphanda fusca	1/10	Tro	*Camponotus* sp.	Oriental/ Palearctic
Polyommatiti				
Chilades lajus	1/17	Hom	?	Japanese
Lepidochrysops (11 spp.)	126/126	Phy/Bro/Tro	*Camponotus*	African
Maculinea (6 spp.)	6/6	Phy/Bro/Tro	*Myrmica*, *Aphaenogaster*	European/ Oriental
Phengaris daitozana, *P. atroguttata*	2/2	Phy/Bro	*Myrmica*	Oriental
Riodininae				
Riodinini				
Nymphiditi				
Setabis lagus	?/27	Hom	?	Neotropical
Eurybiiti				
Alesa amesis	?/5	Hom	*Camponotus*	Neotropical
Audre aurina	?/31	Tro?	*Camponotus*, *Solenopsis*	Neotropical

[a]Number of known and/or presumed entomophagous species/total number of species in genus.

[b]Bro, ant brood; Det, detritus; Eggs, ant eggs; Fung, algae, lichen and fungi; Hom, Homoptera; Hon, homopteran honeydew; Phy, plants; Tro, ant trophallaxis.

species feed on the brood of their dolichoderine or myrmecine ant hosts, and the remainder are thought to have similar life styles (24, 76).

As with the Aphnaeini and Theclini, the Polyommatini include a few phylogenetically isolated entomophagous species, as well as three entomophagous genera that exhibit a uniquely phytopredaceous life history and shift their diet from plants to ants during larval development: *Maculinea*, *Lepidochrysops*, and *Phengaris*. The best known phytopredaceous lycaenids are those in the Palearctic genus *Maculinea* (Polyommatiti: *Glaucopsyche* section) (6, 42, 85–88, 114, 119, 200, 213–220, 225, 235). The larvae feed on flower buds for the first few instars before being carried into *Myrmica* ant nests (or *Aphaenogaster japonica* in Japanese populations of *Maculinea arionides*).

Most *Maculinea* species feed on ant brood, but two, the sister taxa *M. alcon* and *M. rebeli*, feed from ant regurgitations alone. These "cuckoo" species do not impose as great a fitness cost to the ant colony as those that prey directly on ant brood, and it has been hypothesized that they represent a derived feeding strategy (220, 235). A molecular phylogenetic analysis has shown that the two cuckoo species are the sister group to the rest of their congeners, which themselves form a myrmecophagous clade (T.D. Als, personal communication). Thus the phylogeny neither confirms nor refutes the hypothesis that the cuckoo strategy is derived relative to predation.

Why do larvae of *M. rebeli*, *C. dicksoni* (Aphnaeini), and other trophallactic lycaenids accept ant regurgitations while simultaneously offering DNO secretions? *Thestor* and other miletines, presumably entomophagous for longer than their lycaenine counterparts, offer no such rewards. It may be only a matter of time before the lycaenine larvae lose their DNOs, as have some species of *Aloeides* (130). On the other hand, some of these vestigial-seeming DNO secretions may constitute a sophisticated ant-appeasement strategy, as described earlier in the work by Wada et al. (228) on *N. fusca*.

Most species of *Maculinea* are highly specific with respect to their ant associates, with highest survivorship in the nests of one particular ant species (217). The obligate, host-specific aspects of this association have been invoked to explain the small population sizes and threatened conservation status characteristic of most *Maculinea* species (86, 114).

Two species of *Phengaris*, an Oriental genus in the same section and probably closely related to *Maculinea*, share a similar life history (223). Larvae of *Phengaris daitozana* feed within *Tripterospermum* flower buds until the third instar, when they are transported by workers into a *Myrmica* colony where they grow and pupate. *Phengaris atroguttata formosana* uses related plants and ants, and the larvae of both species feed on ant brood in their later instars (223).

The phytopredaceous life history observed within the genus *Lepidochrysops* (*Euchrysops* section) is convergent with that of *Maculinea* (*Glaucopsyche* section), although further phylogenetic work will be necessary to clarify the relationship. Species in both genera are similar in lacking TOs and using their DNO secretions to appease ants before entering the underground entomophagous phase (130).

Restricted to Africa, *Lepidochrysops* is an unusually large genus. Reliable life histories have been published for only 11 of the 126 recognized species, with the remainder assumed to be ecologically similar (37, 41, 47, 131, 132, 239). A taxonomic revision may reveal considerably fewer than 126 true species in the genus, and a rigorous phylogeny of *Lepidochrysops* and its related genus *Euchrysops* has yet to be done. The two genera are currently differentiated almost solely on the basis of life history, with *Euchrysops* species grouped by their limited myrmecophily. A reliable phylogeny of this section combined with more comprehensive life history accounts could reveal multiple origins of entomophagy rather than one large radiation.

From Mutualism to Parasitism

In the large subfamily Lycaeninae, entomophagous species are most often distributed singly or in small clades. This pattern indicates that convergent shifts from exclusive phytophagy to entomophagy have occurred relatively frequently and suggests a lack of phylogenetic constraint against such shifts. Moreover, parasitic entomophagous species typically emerge from within mutualistically ant-associated groups, with the exception of *Shirozua* within the weakly ant-associated Thecliti. Entomophagy does not appear at all in the largely myrmecoxenous Lycaenini. The reverse trend, a single phytophagous species occuring within an otherwise entomophagous clade, is never observed. The Riodininae exhibit a comparable pattern, although their life histories are much less well known. Entomophagy has been recorded for only a few species in this subfamily (∼1200 spp. total), but these species fall within the ant-associated subtribes Eurybiiti and Nymphidiiti (including Lemoniiti) (63, 177).

Evolutionary Constraints on Entomophagy

Although entomophagy occurs frequently in the Lycaenidae, it most often appears as a species-poor dead end. Of the approximately 160,000 species in the Lepidoptera, well over 99% are strictly phytophagous as larvae (189). This is among the highest proportions of phytophagy in a large insect clade, comparable only to groups such as the Orthoptera (>99% phytophagous), Hemiptera (90.7%), and Phytophaga [within Coleoptera; >99% (210)]. The larvae of about 500 lepidopteran species have been observed or inferred to feed on other arthropods or arthropod exudates; these species are widely dispersed across the lepidopteran phylogeny, with few large clades characterized by such a feeding mode (183). These small phylogenetically disparate groups include ∼200 moth species (183).

Of the remaining species, the majority are lycaenids, pointing to ant association as a frequent precondition for lepidopteran entomophagy. Approximately 300 lycaenids are known or suspected to be entomophagous. Most of these occur within the Miletinae and the polyommatine genus *Lepidochrysops*, leaving only about 40 species of entomophages scattered across the rest of the phylogeny.

With the exception of the two radiations described above, Miletinae and *Lepidochrysops*, entomophagy seems to be a short-lived evolutionary experiment. Possible causes are problems associated with life cycle complexity and with phylogenetic/physiological constraint (183). Over one third of the 152 lycaenid species in the IUCN Red List of Threatened Species (36) are entomophagous. Although this disproportionately high representation is in part due to heavy listing of *Lepidochrysops* and *Thestor* species, it accords with the phylogenetic pattern. The phylogeny suggests that entomophagy is an extinction-prone dead end, and demographic studies seem to confirm this.

The conservation consequences of entomophagy point to ant association as a double-edged sword for lycaenid butterflies. Association with ants has promoted rapid rates of diversification in the Lycaenidae, with an overlapping mosaic of ant and plant distributions yielding small isolated populations—the raw material of speciation. While population fragmentation may have resulted in a net diversification over evolutionary time, it simultaneously increases the risk of local extinction. In the face of anthropogenic disturbance and habitat loss, the balance may be tipping toward ever-higher extinction rates among lycaenid butterflies. This is true not only for entomophagous species such as the Large Blue (*Maculinea arion*) in the United Kingdom, Arionides Blue (*M. arionides*) in Japan, and the Mangrove Ant-Blue (*A. illidgei*) in Australia, but increasingly for phytophagous species such as the Brenton Blue (*Orachrysops niobe*) in South Africa, and the Karner Blue (*Lycaeides melissa samuelis*) in the United States (7). With their highly complex life histories, it is not surprising that lycaenids are particularly sensitive to perturbations of their environment (173).

BIOGEOGRAPHIC DISTRIBUTION

Zoogeographical Patterns in Ant Association

A number of lycaenid lineages have their centers of distribution in particular zoogeographic regions (Table 3). Pierce (181) estimated the prevalence of ant associations in different zoogeographic regions based on data summarized from regional faunistic surveys. This analysis showed a striking discrepancy in the extent of ant associations between regions, with obligate interactions much more common in the Southern Hemisphere than in the Northern Hemisphere.

Subsequent studies have shown that the proportion of facultative ant associates in Europe and North West Africa may be higher than originally estimated (96). However, revised estimates of the proportion of the three main types of ant association still confirm that the incidence of obligate associations is far more prevalent in the Australian, Afrotropical, and Oriental Regions than in the Holarctic (Table 4). Australia (39%) and southern Africa (59%) have especially high levels of obligate ant association. By contrast, obligate myrmecophily in the Nearctic is less than 2%, and ant association in general is rare, with over 80% of the species apparently not associating with ants. Life histories of over half the species in the Oriental

TABLE 3 The geographical distribution of the major lycaenid taxonomic groups (subfamilies and tribes) within each zoogeographic region

Taxonomic group	Zoogeographical region					
	Australian	Afrotropical	Oriental	Palaearctic	Nearctic	Neotropical
PORITIINAE						
Poritiini			+++			
Pentilini		+++				
Liptenini		+++				
MILETINAE						
Liphyrini	+	++	+			
Miletini	+	+	+++			
Spalgini		+	+	+	+	
Lachnocnemini		+++				
CURETINAE	+		++	+		
LYCAENINAE						
Theclini	++++	+	++++	+++	+++	++++
Aphnaeini		++++	++	++		
Lycaenini	+	+	++	+++	++	+
Polyommatini	+++	++++	++++	++++	+++	+++
RIODININAE	++	++	++	++	++	++++

+, low representation in region (1–4 species); ++, moderate representation (5–30 species); +++, high representation (31–100 species); ++++, very high representation (>100 species).

Data derived from Eliot (83), DeVries (63), and Fiedler (95). Several authors recognize an additional tribe, Eumaeini, consisting mainly of subtribes within the Theclini, but in the absence of additional phylogenetic information we have retained Eliot's broader definition of Theclini.

Region are presently unknown, but the region appears to be transitional between the southern and northern regions in the percentage of obligate association. Our understanding of life histories of Lycaenidae in the Neotropics is poor relative to other geographic regions, and broad systematic analyses are still forthcoming. We have therefore not included the Neotropical fauna in most of our discussion here (but see 13, 14, 28–32, 50, 61, 63, 65, 121–124, 147, 148, 170, 177, 192–194, and references therein).

At least two nonexclusive factors account for these pronounced biogeographical differences in obligate ant association. One is the systematic composition of the major taxonomic groups within each region and concomitant levels of myrmecophily. The other concerns ecological factors or selective forces that may have led to the loss or gain of myrmecophily in particular clades.

Phylogenetic Patterns in Ant Association

Pierce (181) noted that all but one of the recognized tribes of the Lycaenidae (*sensu* Eliot 1973) can be found in both the Holarctic and the southern regions, and most of the tribes contain both ant-associated and non-ant-associated species.

TABLE 4 The number and proportion (in parentheses) of ant-associated species in each major zoogeographic region (comparable data for the Neotropical region not available)

Zoogeographical region	N	Ant-association (%)			Source
		Obligate	**Facultative**	**None**	
Australian					
Australia	128	50 (39)	51 (40)	27 (21)	(24, 77)
Afrotropical					
Southern Africa	160	94 (59)	28 (17)	34 (24)	Heath[a]
Oriental					
India	60	13 (22)	32 (53)	15 (25)	(21)
	114	12 (10)	78 (69)	24 (21)	(95)
Malay Peninsula and Borneo	134	35 (26)	86 (64)	13 (10)	(103)
Palaearctic					
Europe and NW Africa	82	10 (12)	55 (67)	17 (20)	(94)
	121	9 (7)	88 (73)	24 (20)	(103)
Japan	72	5 (7)	20 (28)	47 (65)	(181)
Nearctic					
United States	126	1 (1)	22 (17)	103 (82)	(181)
Canada	64	1 (2)	7 (11)	56 (87)	(159)

[a]Unpublished data; see also reference in Table 4.

Thus a single vicariance event involving ant-associated versus non-ant-associated lineages could not explain the dichotomy in obligate ant association observed between the Holarctic and Southern Hemisphere regions. However, an analysis of lower taxonomic levels (tribes and subtribes) using additional life history records showed a strong correlation between the degree of ant association and systematic group (95; Table 1). The geographically heterogeneous distribution of tribes with different levels of ant association can explain much of the observed faunal split.

The correlation between ant association and phylogeny in Australia and southern Africa can be seen more clearly when the lower taxonomic categories (tribes, subtribes) are analyzed in detail (Table 5). The high degree of obligate associations in the Australian and Afrotropical regions is associated with the presence of the Theclini and Aphnaeini, respectively. In contrast, the low level of obligate associations in the Palaearctic and Nearctic correlates with the preponderance of the Lycaenini and non-ant-associated subtribes of Theclini, respectively, as well as the ubiquitous Polyommatini.

In a sense, however, this only pushes back by one level the analysis of the causation of the geographical heterogeneity in ant association. Obligately ant-associated groups are more numerous in the Southern Hemisphere, and the question remains

TABLE 5 The number and proportion (in parentheses) of ant-associated species within each lycaenid taxonomic group (subfamilies, tribes, subtribes) in Australia and Southern Africa

Taxonomic group	N	Australia Ant-association (%) Obligate	Facultative	None	N	Southern Africa Ant-association (%) Obligate	Facultative	None
PORITIINAE					23	0	0	23 (100)
Poritiini					0	0	0	0
Pentilini					8	0	0	8 (100)
Liptenini					15	0	0	15 (100)
MILETINAE	1	1 (100)	0	0	15	8 (53)	0	7 (47)
Liphyrini	1	1 (100)	0	0	3	0	0	3 (100)
Miletini					8	8 (100)	0	0
Spalgini					1	0	0	1 (100)
Lachnocnemini					3	0	0	3 (100)
LYCAENINAE	126	49 (39)	51 (40)	26 (21)	122	86 (70)	28 (23)	8 (7)
Theclini	68	48 (70)	10 (15)	10 (15)	17	0	17 (100)	0
Luciiti	31	23 (74)	3 (10)	5 (16)				
Arhopaliti	4	4 (100)	0	0				
Ogyriti	13	9 (69)	4 (31)	0				
Zesiiti	11	11 (100)	0	0				
Amblypodiiti					2	0	2 (100)	0
Iolaiti					4	0	4 (100)	0
Hypolycaeniti	2	1 (50)	0	1 (50)	4	0	4 (100)	0
Deudorigiti	7	0	3 (43)	4 (47)	7	0	7 (100)	0
Aphnaeini					79	78 (99)	1 (1)	0
Lycaenini					2	0	0	2 (100)
Polyommatini	58	1 (2)	41 (71)	16 (27)	24	8 (33)	10 (42)	6 (25)
Lycaenesthiti	2	1 (50)	1 (50)	0	4	2 (50)	2 (50)	0
Candaliditi	16	0	12 (75)	4 (25)				
Polyommatiti	40	0	28 (70)	12 (30)	20	6 (30)	8 (40)	6 (30)
RIODININAE	1	0	0	1 (100)				
Total	128	50 (39)	51 (40)	27 (21)	160	94 (59)	28 (17)	38 (24)

Data derived from Eastwood & Fraser (77) and Braby (24) for Australia; Jackson (145, 146), Clark & Dickson (41), Schlosz & Brinkman (199), Heath & Claassens (130), Heath (125), and Heath (unpublished data) for Southern Africa.

as to why this is the case. Are there phylogeographic features that have enhanced the success of ant-associated lineages in these regions?

Ecological factors undoubtedly influence the extent of ant association within zoogeographic regions or within clades. In the Western Palaearctic, for example, the proportion of facultative myrmecophilous species decreases with increasing latitude, and in the boreal and tundra zones ant association is rare (103). However, this same pattern of decreasing myrmecophily with increasing latitude was not observed in Australia (181). The phosphorus-poor soils of southern Africa and Australia may have played a role in the high incidence of ant-dispersed myrmeco-chorous plants in these areas (237), and further research might explore the comparative phylogeny and biogeography of myrmecochorous plants or of ant plants in general. For example, whereas the genus *Macaranga* has a wide distribution

in the Old World tropics, the clade containing ant plants seems to be confined to West Malesian rainforest, a region well known for its phosphorus-poor soils (51).

Origin and Evolution of Ant Association

Hinton (139, pp. 122) noted that "the possession of a dorsal organ appears to be a primitive feature in the Lycaenidae, and, if this is indeed the case, it follows that its absence is in all cases secondary." However, Fiedler (95) argued that because the putatively ancestral lycaenid lineages (Poritiinae + Miletinae + Curetinae) are not generally ant associated, myrmecophily is a derived state in the sister clade Lycaeninae. This assumes that the ant-associated taxa observed in the Riodininae and myrmecophagous Miletinae have arisen independently. In either case, within the subfamily Lycaeninae, absence of overt ant association can be found among species in nearly all tribes, suggesting that putative losses or gains of myrmecophily have occurred multiple times.

Analyzing the evolution of ant association within and between different lineages of the Lycaenidae remains problematic, and given the numerous gains and losses that have occurred, we may never know the sequence of events. The possession of PCOs, thought to be used in appeasing and/or otherwise chemically manipulating ants, is a synapomorphy in all subfamilies of the Lycaenidae, including Riodininae (44). A reasonable conclusion is that manipulation of ants was an important first step in the evolution of myrmecophilous interactions, whether mutualistic or parasitic. It may have been the crucial step necessary for the Miletinae to evolve homopterophagy through the appeasement of otherwise aggressive ants and possibly through the use of the ants themselves as cues in finding prey.

Based on consideration of species richness and present-day distributions, Eliot (83) hypothesized that the Lycaenidae arose in the mid-Cretaceous (ca. 100 million years ago) and were Gondwanan in origin. The Oriental and Afrotropical Regions contain the greatest phylogenetic diversity, including the putatively ancestral Poritiinae, Miletinae, and Curetinae, whereas the vast majority of the Riodininae occur in the Neotropical Region. In comparison, the Holarctic fauna is systematically depauperate and is more recently derived from the Old World (via Asia and possibly Africa) and possibly South America (but see 148). The origin of the Oriental fauna and the role of India are uncertain. Eliot (83) suggested that lycaenids were absent on India during its northward drift from Antarctica and that the Southeast Asian fauna was derived from Africa through invasion by dispersal, possibly via India. If the Oriental fauna is older than hitherto believed, and the Poritiini and Curetinae represent relictual groups, a scenario of secondary radiation after contact with India in the early Tertiary (and later with Australia in the late Tertiary) seems plausible.

A southern origin of the Papilionoidea is not widely accepted (e.g., 203, 204); however, several studies advocate the presence of butterflies in Gondwana prior to continental breakup (95, 168, 176; see also 143). An analysis of the endemic Australian butterfly fauna (24) supports the presence of ancient (relictual) and more

recently derived Gondwanan elements. Several components of the largely endemic Theclini subtribes (Luciiti, Ogyriti, and Zesiiti) are temperate in distribution and specialize on Gondwanan plants. These groups also contain exceedingly high proportions of obligately ant-associated species.

This fact, along with the high level of obligate ant association observed in Africa, suggest that the Australian Theclini and the African Aphnaeini may represent ancient vicariant myrmecophilous lineages within the Lycaeninae. Together with the present-day distributions of other major groups, this points toward a southern origin of the Lycaenidae. As a corollary, the Polyommatini, New World Eumaeiti, and Lycaenini are possibly more derived, and the latter tribe, which shows reduced myrmecophily and does not form obligate associations with ants, may have originated in the Northern Hemisphere. Such a phylogeographic model is not inconsistent with the low incidence of obligate myrmecophily in the Palaearctic and Nearctic.

Determining the phylogenetic relationships and monophyly of the major lineages are a priority if we are to understand the evolution of ant association in this group of butterflies. If, as originally suggested by Eliot, the Holarctic fauna was derived from the southern areas and loss of myrmecophily is derived, a prediction is that the Aphnaeini + certain subtribes of Theclini are basal and the Lycaenini + Eumaeiti + Polyommatini are derived groups within the Lycaeninae. Critical to understanding the origin of the Lycaenidae and the evolution of ant associations will be the elucidation of systematic relationships and larval-ant associations in South America. The systematics and biology of species in this part of the world are still poorly known, and the Eumaeiti, of which more than 900 species are endemic (95), may be paraphyletic. If a Gondwana faunal split did play a role in the evolution of the lycaenids, some of these taxa may be highly ant associated and have close relatives in southern Africa and Australia.

CONCLUSIONS

The Lycaenidae provide a model system for studying the evolution of complex species interactions. The behavioral and ecological diversity of this group makes it particularly amenable for comparative studies. However, the validity of conclusions drawn from such comparisons is called into question by our poor understanding of the evolutionary history of the family at almost every level. A detailed phylogeny of Lycaenidae and related groups is essential if we are to evaluate these hypotheses. Without more information regarding their evolutionary history, quantitative comparisons of lycaenid behavioral and ecological attributes are at best difficult to interpret.

The possibility that ant association has both promoted and constrained diversification of the Lycaenidae could be evaluated through additional analysis of targeted groups. Comparisons of population structure between ant-associated and non-ant-associated species may reveal mechanisms underlying rates of speciation

and extinction in different lineages. The development, chemistry, function, and evolution of ant-associated organs require much further work. The biogeographic predominance of obligately myrmecophilous lycaenids in the Southern Hemisphere remains unexplained, and an understanding of this distribution will require a combined phylogenetic and ecological approach. Finally, exploration of the systematics and natural history of the Neotropical fauna is essential for our understanding of the origin and evolution of the Lycaenidae and their symbioses with ants.

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LITERATURE CITED

1. Ackery PR, de Jong R, Vane-Wright RI. 1999. The butterflies: Hedyloidea, Hesperoidea, and Papilionoidea. *Handb. Zool.* 4:263–300

2. Agrawal AA, Fordyce JA. 2000. Induced indirect defence in a lycaenid-ant association: the regulation of a resource in a mutualism. *Proc. R. Soc. London Ser. B* 267:1857–61

3. Akino T, Knapp JJ, Thomas JA, Elmes GW. 1999. Chemical mimicry and host specificity in the butterfly *Maculinea rebeli*, a social parasite of *Myrmica* ant colonies. *Proc. R. Soc. London Ser. B* 266:1419–26

4. Akre RD, Rettenmeyer CW. 1968. Trail-following by guests of army ants (Hymenoptera: Formicidae: Ecitonini). *J. Kans. Entomol. Soc.* 41:165–74

5. Allan RA, Elgar MA, Capon RJ. 1996. Exploitation of an ant chemical alarm signal by the zodariid spider *Habronestes bradleyi* Walckenaer. *Proc. R. Soc. London Ser. B* 263:69–73

6. Als TD, Nash DR, Boomsma JJ. 2001. Adoption of parasitic *Maculinea alcon* caterpillars (Lepidoptera: Lycaenidae) by three *Myrmica* ant species. *Anim. Behav.* 62:99–106

7. Andow DA, Baker RJ, Lane CP, eds. 1994. *Karner Blue Butterfly: A Symbol of a Vanishing Landscape*. St. Paul, MN: Minn. Agric. Exp. Stn. 222 pp.

8. Arnquist G. 1998. Comparative evidence for the evolution of genitalia by sexual selection. *Nature* 393:784–86

9. Atsatt PR. 1981. Ant-dependent food plant selection by the mistletoe butterfly *Ogyris amaryllis* (Lycaenidae). *Oecologia* 48:60–63

10. Atsatt PR. 1981. Lycaenid butterflies and ants: selection for enemy-free space. *Am. Nat.* 118:638–54

11. Axén AH, Leimar O, Hoffman V. 1996. Signalling in a mutualistic interaction. *Anim. Behav.* 52:321–33

12. Axén AH, Pierce NE. 1998. Aggregation as a cost-reducing strategy for lycaenid larvae. *Behav. Ecol.* 9:109–15

13. Balint Z, Johnson K, Benyamini D. 1995. *Neotropical Blue Butterflies*. Stevens Point, WI: Univ. Wisc. 184 pp.

14. Balint Z, Johnson K. 1997. Reformation of the *Polyommatus* section with a taxonomic and biogeographic overview (Lepidoptera, Lycaenidae, Polyommatini). *Neue Entomol. Nachr.* 40:1–68

15. Ballmer GR, Pratt GF. 1988. A survey of the last instar larvae of the Lycaenidae of California. *J. Res. Lepid.* 27:1–81

16. Ballmer GR, Pratt GF. 1989. Instar number and larval development in *Lycaena phlaeas hypophlaeas* Boisduval (Lycaenidae). *J. Lepid. Soc.* 43:59–65

17. Ballmer GR, Pratt GF. 1992. Quantification of ant attendance (myrmecophily) of lycaenid larvae. *J. Res. Lepid.* 30:95–112

18. Banno H. 1990. Plasticity of size and fecundity in the aphytophagous lycaenid butterfly, *Taraka hamada. Ecol. Entomol.* 15:111–13

19. Baylis M, Pierce NE. 1991. The effect of host-plant quality on the survival of larvae and oviposition by adults of an antended lycaenid butterfly, *Jalmenus evagoras. Ecol. Entomol.* 16:1–9

20. Baylis M, Pierce NE. 1992. Lack of compensation by final instar larvae of the myrmecophilous lycaenid butterfly, *Jalmenus evagoras*, for the loss of nutrients to ants. *Physiol. Entomol.* 17:107–14

21. Bell TR. 1915–1920. The common butterflies of the plains of India. *J. Bombay Nat. Hist. Soc.* 23–27:481–97

22. Bink FA. 1992. *Ecologische Atlas van der Dagvlinders van Noordwest-Europa*. Haarlem, the Netherlands: Schuyt. 512 pp.

23. Blum M. 1969. Alarm pheromones. *Annu. Rev. Ecol. Syst.* 4:57–80

24. Braby MF. 2000. *Butterflies of Australia: Their Identification, Biology and Distribution*. Collingwood: CSIRO. 976 pp.

25. Bradshaw JWS, Baker R, Howse PE. 1979. Multicomponent alarm pheromones in the mandibular glands of major workers of the African weaver ant, *Oecophylla longinoda. Physiol. Entomol.* 4:15–25

26. Brakefield PM, Shreeve TG, Thomas JA. 1992. Avoidance, concealment, and defence. In *The Ecology of Butterflies in Britain*, ed. RLH Dennis, pp. 93–119. Oxford: Oxford Univ. Press

27. Brian MV. 1975. Larval recognition by workers of the ant *Myrmica. Anim. Behav.* 23:745–56

28. Brown KS. 1993. Neotropical Lycaenidae: an overview. *Occ. Paper IUCN Species Surviv. Comm.* 8:45–61

29. Callaghan CJ. 1985. A preliminary revision of the genus *Nymphidium* (Rhopalocera, Riodinidae). Part I. Introduction: *Mantus-Baoetia* complex. *Bull. Allyn Mus.* 98:1–21

30. Callaghan CJ. 1986. A preliminary revision of the genus *Nymphidium* (Riodinidae). Part II. The azanoides complex. *Bull. Allyn Mus.* 100:1–7

31. Callaghan CJ. 1988. A preliminary revision of the genus *Nymphidium* (Riodinidae). Part III. The *omois* group. *Bull. Allyn Mus.* 119:1–6

32. Callaghan CJ. 1997. A revision of the *Euselasia orfita* complex (Riodinidae). *J. Lep. Soc.* 51:62–74

33. Cammaerts R, Detrain C, Cammaerts M-C. 1990. Host trail following by the myrmecophilous beetle *Edapaussus favieri* (Fairmaire) (Carabidae, paussinae). *Insectes Soc.* 37:200–11

34. Campbell DL. 1998. *Higher-level phylogeny and molecular evolution of the Riodinidae* (*Lepidoptera*). PhD thesis. Harvard Univ. 137 pp.

35. Campbell DL, Brower AVZ, Pierce NP. 2000. Molecular evolution of the *wingless* gene and its implications for the phylogenetic placement of the butterfly family Riodinidae (Lepidoptera: Papilionoidea). *Mol. Biol. Evol.* 17:684–96

36. Centre WCM. 2000. Threatened animals of the world: http://www.wcmc.org.uk/data/database/rl_anml_combo.html

37. Claassens AJM. 1976. Observations on the myrmecophilous relationships and the parasites of *Lepidochrysops methymna methymna* (Trimen) and *L. trimeni* (Bethune-Baker) (Lepidoptera: Lycaenidae). *J. Entomol. Soc. S. Afr.* 39:279–89

38. Claassens AJM, Dickson CGC. 1977. A study of the myrmecophilous behaviour of the immature stages of *Aloeides thryra* (L.) (Lep.: Lycaenidae) with special reference to the function of the retractile tubercles and with additional notes of the general biology of the species. *Entomol. Rec. J. Var.* 89:253–58

39. Claassens AJM, Dickson CGC. 1980. *Butterflies of the Table Mountain Range*. Cape Town: Struik. 160 pp.

40. Clark GC, Dickson CGC. 1960. The life-histories of two species of *Thestor* (Lepidoptera: Lycaenidae). *J. Entomol. Soc. S. Afr.* 23:278–83

41. Clark GC, Dickson CGC. 1971. *Life Histories of the South African Lycaenid Butterflies*. Cape Town: Purnell. 272 pp.

42. Clarke RT, Thomas JA, Elmes GW, Hochberg ME. 1997. The effects of spatial patterns in habitat quality on community dynamics within a site. *Proc. R. Soc. London Ser. B* 264:347–54

43. Common IFB, Waterhouse DF. 1981. *Butterflies of Australia*. Sydney: Angus & Robertson. 682 pp.

44. Corbet AS, Pendlebury HM, Eliot JN. 1992. *The Butterflies of the Malay Peninsula*. Kuala Lumpur: Malay. Nat. Soc. 595 pp.

45. Costa JT. 1997. Social evolution in the Lepidoptera: ecological context and communication in larval societies. In *The Evolution of Social Behavior in Insects and Arachnids*, ed. JC Choe, BJ Crespi, pp. 407–42. Cambridge, UK: Cambridge Univ. Press

46. Costa JT, McDonald JH, Pierce NE. 1996. The effect of ant association on the population genetic structure of the mutualistic butterfly, *Jalmenus evagoras* (Lepidoptera: Lycaenidae). *Biol. J. Linn. Soc.* 58:287–306

47. Cottrell CB. 1965. A study of the *Methymna* group of the genus *Lepidochrysops* Hedicke (Lepidoptera: Lycaenidae). *Mem. Entomol. Soc. S. Afr.* 9:1–110

48. Cottrell CB. 1984. Aphytophagy in butterflies: its relationship to myrmecophily. *Zool. J. Linn. Soc.* 79:1–57

49. Cushman JH, Rashbrook VK, Beattie AJ. 1994. Assessing benefits to both participants in a lycaenid-ant association. *Ecology* 75:1031–41

50. D'Abrera B. 1995. *Butterflies of the Neotropical Region. Pt.7; Lycaenidae*. Victoria, Aust.: Hill House. 168 pp.

51. Davies SJ, Lum SKY, Chan R, Wang LK. 2001. Evolution of myrmecophytism in West Malesian *Macaranga* (Euphorbiaceae). *Evolution* 55:1542–59

52. De Barr M. 1984. Sound production by lycaenid larvae (Lepidoptera). *Entomol. Soc. Qld.* 12:74–75

53. De Barr M. 1985. The complex mistletoe-insect community. *Entomol. Soc. Qld. News. Bull.* 13:100–2

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

55. de Jong R, Vane-Wright RI, Ackery PR. 1996. The higher classification of butterflies (Lepidoptera): problems and prospects. *Entomol. Scand.* 27:65–101

56. DeVries PJ. 1984. Of crazy-ants and Curetinae: Are *Curetis* butterflies tended by ants? *Zool. J. Linn. Soc.* 79:59–66

57. DeVries PJ. 1988. The larval ant-organs of *Thisbe irenea* (Lepidoptera: Riodinidae) and their effects upon attending ants. *Zool. J. Linn. Soc.* 94:379–93

58. DeVries PJ. 1989. Detecting and recording the calls produced by butterfly caterpillars and ants. *J. Res. Lepid.* 28:258–62

59. DeVries PJ. 1990. Enhancement of symbiosis between butterfly caterpillars and

ants by vibrational communication. *Science* 248:1104–6

60. DeVries PJ. 1991. Call production by myrmecophilous riodinid and lycaenid butterfly caterpillars (Lepidoptera): morphological, acoustical, functional, and evolutionary patterns. *Am. Mus. Nov.* 3025:1–23

61. DeVries PJ. 1991. Evolutionary and ecological patterns in myrmecophilous riodinid butterflies. In *Ant-Plant Interactions*, ed. CR Huxley, DF Cutler, pp. 143–56. Oxford: Oxford Univ. Press

62. DeVries PJ. 1991. The mutualism between *Thisbe irenea* and ants, and the role of ant ecology in the evolution of larval-ant associations. *Biol. J. Linn. Soc.* 43:179–95

63. DeVries PJ. 1997. *The Butterflies of Costa Rica and their Natural History. Volume II: The Riodinidae*. Princeton, NJ: Princeton Univ. Press

64. DeVries PJ, Baker I. 1989. Butterfly exploitation of an ant-plant mutualism: adding insult to herbivory. *J. NY Entomol. Soc.* 97:332–40

65. DeVries PJ, Chacon IA, Murray D. 1992. Toward a better understanding of host use and biodiversity in riodinid butterflies (Lepidoptera). *J. Res. Lepid.* 31:103–26

66. DeVries PJ, Cocroft RB, Thomas J. 1993. Comparison of acoustical signals in *Maculinea* butterfly caterpillars and their obligate host *Myrmica* ants. *Biol. J. Linn. Soc.* 49:229–38

67. DeVries PJ, Harvey DJ, Kitching IJ. 1986. The ant associated epidermal organs on the larva of the lycaenid butterfly *Curetis regula* Evans. *J. Nat. Hist.* 20:621–33

68. DeVries PJ, Penz CM. 2000. Entomophagy, behavior, and elongated thoracic legs in the myrmecophilous neotropical butterfly *Alesa amesis* (Riodinidae). *Biotropica* 32:712–21

69. Dodd FP. 1902. Contribution to the life-history of *Liphyra brassolis*, Westw. *Entomologist* 35:153–88

70. Dornfeld EJ. 1980. *The Butterflies of Oregon*. Forest Grove, OR: Timber Press. 276 pp.

71. Downey JC. 1966. Sound production in pupae of Lycaenidae. *J. Lepid. Soc.* 20:129–55

72. Downey JC, Allyn AC. 1973. Butterfly ultrastructure: 1. Sound production and associated abdominal structures in pupae of Lycaenidae and Riodinidae. *Bull. Allyn Mus. Entomol.* 14:1–39

73. Downey JC, Allyn AC. 1978. Sounds produced in pupae of Lycaenidae. *Bull. Allyn Mus. Entomol.* 48:1–14

74. Downey JC, Allyn AC. 1979. Morphology and biology of the immature stages of *Leptotes cassius theonus* (Lucas) (Lepidoptera: Lycaenidae). *Bull. Allyn Mus. Entomol.* 55:1–27

75. Eastwood R. 1997. Field observations on the symbiotic interactions of *Ogyris genoveva* (Hewitson) and *Ogyris zosine* (Hewitson) (Lepidoptera: Lycaenidae) with *Camponotus* spp. (Hymenoptera: Formicidae). *Aust. Entomol.* 24:137–43

76. Eastwood R. 2001. *Molecular phylogeny and phylogeography of* Acrodipsas *(Lepidoptera: Lycaenidae)*. Honours thesis. Griffith Univ., Qld. 159 pp.

77. Eastwood R, Fraser A. 1999. Associations between lycaenid butterflies and ants in Australia. *Aust. J. Ecol.* 24:503–37

78. Eastwood R, King AJ. 1998. Observations on the biology of *Arhopala wildei* Miskin (Lepidoptera: Lycaenidae) and its host ant *Polyrhachis queenslandica* (Hymenoptera: Formicidae). *Aust. Entomol.* 25:1–6

79. Ebert G, E. R. 1991. *Die Schmetterlinge Baden-Württembergs*, *Band 2: Tagfalter II*. Stuttgart: Ulmer. 535 pp.

80. Ehrlich PR, Raven PH. 1964. Butterflies and plants: a study in coevolution. *Evolution* 18:586–608

81. Elfferich NW. 1988. Gerauschproduktion bei Lycaeniden-puppen (Lepidoptera). *Mitt. Entomol. Ges. Basel* 38:156–68

82. Elgar MA, Pierce NE. 1988. Mating success and fecundity in an ant-tended lycaenid butterfly. In *Reproductive Success:*

Studies of Selection and Adaptation in Contrasting Breeding Systems, ed. TH Clutton-Brock, pp. 59–75. Chicago: Univ. Chicago Press

83. Eliot JN. 1973. The higher classification of the Lycaenidae (Lepidoptera): a tentative arrangement. *Bull. Brit. Mus. Nat. Hist.* (*Entomol.*) 28:371–505

84. Eliot JN. 1990. Notes on the genus *Curetis* Hübner (Lepidoptera, Lycaenidae). *Tyô to Ga* 41:201–25

85. Elmes GW, Clarke RT, Thomas JA, Hochberg ME. 1996. Empirical tests of specific predictions made from a spatial model of the population dynamics of *Maculinea rebeli*, a parasitic butterfly of red ant colonies. *Acta Oecol.* 17:61–80

86. Elmes GW, Thomas JA. 1992. Complexity of species conservation in managed habitats: interaction between *Maculinea* butterflies and their ant hosts. *Biodivers. Conserv.* 1:155–69

87. Elmes GW, Thomas JA, Munguira ML, Fiedler K. 2001. Larvae of lycaenid butterflies that parasitize ant colonies provide exceptions to normal insect growth rules. *Biol. J. Linn. Soc.* 73:259–78

88. Elmes GW, Thomas JA, Wardlaw JC. 1991. Larvae of *Maculinea rebeli*, a large-blue butterfly, and their *Myrmica* host ants: wild adoption and behaviour in ant-nests. *J. Zool. London* 223:447–60

89. Emmel TC, Emmel JF. 1973. *The Butterflies of Southern California*. Los Angeles: Nat. Hist. Mus. Los Angel. 334 pp.

90. Ewing AW. 1984. Insect communication. In *Insect Communication*, ed. T Lewis, pp. 223–40. London: Academic

91. Farquharson CO. 1921. 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. *Trans. Entomol. Soc. London* 1921:319–448

92. Felsenstein J. 1985. Phylogenies and the comparative method. *Am. Nat.* 125:1–15

93. Ferris CD, Brown FM. 1981. *Butterflies of the Rocky Mountain States*. Norman, OK: Univ. Okla. Press

94. Fiedler K. 1990. Effects of larval diet on the myrmecophilous qualities of *Polyommatus icarus* caterpillars (Lepidoptera, Lycaenidae). *Oecologia* 83:284–87

95. Fiedler K. 1991. Systematic, evolutionary, and ecological implications of myrmecophily within the Lycaenidae (Insecta: Lepidoptera: Papilionoidea). *Bonn. Zool. Monogr.* 31:5–157

96. Fiedler K. 1991. European and North West African Lycaenidae (Lepidoptera) and their associations with ants. *J. Res. Lepid.* 28:239–57

97. Fiedler K. 1992. Notes on the biology of *Hypolycaena othona* (Lepidoptera: Lycaenidae) in West Malaysia. *Nachr. Entomol. Vereins Apollo* 13:65–92

98. Fiedler K. 1992. The life-history of *Surendra florimel* Doherty 1889 (Lepidoptera: Lycaenidae) in West Malaysia. *Nachr. Entomol. Vereins. Apollo* 113:107–35

99. Fiedler K. 1994. Lycaenid butterflies and ants: is myrmecophily associated with amplified hostplant diversity? *Ecol. Entomol.* 19:79–82

100. Fiedler K. 1994. The life-history of *Caleta roxus* (Lepidoptera: Lycaenidae). *Nachr. Entomol. Vereins Apollo* 14:371–84

101. Fiedler K. 1995. Lycaenid butterflies and plants: is myrmecophily associated with particular hostplant preferences? *Ethol. Ecol. Evol.* 7:107–32

102. Fiedler K. 1996. Host-plant relationships of lycaenid butterflies: large-scale patterns, interactions with plant chemistry, and mutualism with ants. *Entomol. Exp. Appl.* 80:259–67

103. Fiedler K. 1998. Geographical patterns in life-history traits of Lycaenidae butterflies—ecological and evolutionary patterns. *Zoology* 100:336–47

104. Fiedler K. 1998. Lycaenid-ant interactions of the *Maculinea* type: tracing their historical roots in a comparative framework. *J. Insect Conserv.* 2:3–14

105. Fiedler K, Hölldobler B. 1992. Ants and *Polyommatus icarus* immatures (Lycaenidae): sex-related developmental benefits and costs of ant attendance. *Oecologia* 91:468–73

106. Fiedler K, Hölldobler B, Seufert P. 1996. Butterflies and ants: the communicative domain. *Experientia* 52:14–24

107. Fiedler K, Maschwitz U. 1988. 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* 75:204–6

108. Fiedler K, Maschwitz U. 1989. Adult myrmecophily in butterflies: the role of the ant *Anoplolepis longipes* in the feeding and oviposition behaviour of *Allotinus unicolor*. *Tyô to Ga* 40:241–51

109. Fiedler K, Maschwitz U. 1989. The symbiosis between the weaver ant, *Oecophylla smaragdina*, and *Anthene emolus*, an obligate myrmecophilous lycaenid butterfly. *J. Nat. Hist.* 23:833–46

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

111. Fiedler K, Saam C. 1995. A "microbial cost" of butterfly-ant mutualisms (Lycaenidae). *J. Lepid. Soc.* 49:80–84

112. Fiedler K, Seufert P, Maschwitz U, Idris A. 1995. Notes on the larval biology and pupal morphology of Malaysian *Curetis* butterflies. *Tyô to Ga* 45:287–99

113. Fiedler K, Seufert P, Pierce NE, Pearson JG, Baumgarten H. 1992. Exploitation of lycaenid-ant mutualisms by braconid parasitoids. *J. Res. Lepid.* 31:153–68

114. Figurny-Puchalska E, Gadeberg RME, Boomsma JJ. 2000. Comparison of the genetic population structure of the large blue butterflies *Maculinea nausithous* and *M. teleius*. *Biodivers. Conserv.* 9:419–32

115. Forster W, Wohlfahrt TA. 1976. *Die schmetterlinge Mitteleuropas*. Stuttgart: Franckh'sche. 180 pp. 2nd ed.

116. Franzl S, Locke M, Huie P. 1984. Lenticles: innervated secretory structures that are expressed at every other larval moult. *Tissue Cell* 16:251–68

117. Fraser A. 1997. *Evolution of specialization in lycaenid butterfly-ant mutualisms*. PhD thesis. Harvard Univ., Cambridge. 128 pp.

118. Fukuda H, Hama E, Kuzuya T, Takahashi A, Takahashi M, et al. 1984. *The Life Histories of Butterflies in Japan Vol. III*. Osaka: Hoikusha. 373 pp.

119. Gadeberg RME, Boomsma JJ. 1997. Genetic population structure of the large blue butterfly *Maculinea alcon* in Denmark. *J. Insect Conserv.* 1:99–111

120. Gibbs AG. 1998. Water-proofing properties of cuticular lipids. *Am. Zool.* 38:471–82

121. Hall JPW. 1998. A review of the genus *Sarota* (Lepidoptera: Riodinidae). *Trop. Lepid.* 9:1–21

122. Hall JPW. 1999. *A Revision of The Genus Theope: Its Sytematics and Biology*. Gainesville, FL: Sci. Publ. 127 pp.

123. Hall JPW, Wilmott KR. 2000. Patterns of feeding behaviour in adult male riodinid butterflies and their relationship to morphology and ecology. *Biol. J. Linn. Soc.* 69:1–23

124. Harvey D. 1987. *The higher classification of the Riodinidae*. PhD thesis. Univ. Tex., Austin. 215 pp.

125. Heath A. 1997. A review of African genera of the tribe Aphnaeini (Lepidoptera: Lycaenidae). *Metamorph. Occas. Suppl.* 2:1–60

126. Heath A. 1997. Myrmecophily and the male genitalia of African Lycaenidae: a preliminary discussion. *Metamorphosis* (*Suppl.*) 3:89–97

127. Heath A. 1998. Further aspects on the life history of the mymecophilous species *Chrysoritis dicksoni* (Gabriel), (Lepidoptera: Lycaenidae). *Metamorphosis* 9:160–72

128. Heath A, Brinkman AK. 1995. Aspects of the life history, distribution, and

population fluctuations of *Oxychaeta dicksoni* (Gabriel). *Metamorphosis* 6: 117–27

129. Heath A, Brinkman AK. 1995. Notes on the early stages of *Argyrocupha malagrida maryae* (Wallengren) (Lepidoptera, Lycaenidae). *Metamorphosis* 6:167–73

130. Heath A, Claassens AJM. 2000. New observations of ant associations and life history adaptations (Lepidoptera: Lycaenidae) in South Africa. *Metamorphosis* 11:3–18

131. Henning SF. 1983. Biological groups within the Lycaenidae (Lepidoptera). *J. Entomol. Soc. S. Afr.* 46:65–85

132. Henning SF. 1983. Chemical communication between lycaenid larvae (Lepidoptera: Lycaenidae) and ants (Hymenoptera: Formicidae). *J. Entomol. Soc. S. Afr.* 46:341–66

133. Henning SF. 1984. The effect of ant association on lycaenid larval duration (Lepidoptera: Lycaenidae). *Entomol. Rec. J. Var.* 96:99–102

134. Henning SF. 1997. Chemical communication between lycaenid larvae (Lepidoptera: Lycaenidae) and ants (Hymenoptera: Formicidae). *Metamorphosis* (*Suppl.*) 3:66–81

135. Hesselbarth G, van Oorschot H, Wagener S. 1995. *Die Tagfalter der Türkei unter Berücksichtigung der angrenzenden Länder* (*Lepidoptera Papilionoidea and Hesperioidea*), Vols. 1, 2, 3. Bocholt: Wagener. 2201 pp.

136. Higgins LG, Hargreaves B. 1983. *The Butterflies of Britain and Europe*. London: Collins. 256 pp.

137. Higgins LG, Riley ND. 1970. *A Field Guide to the Butterflies of Britain and Europe*. London: Collins. 380 pp.

138. Hill CJ. 1993. The myrmecophilous organs of the butterfly *Arhopala madytus* Fruhstorfer (Lepidoptera: Lycaenidae). *J. Aust. Entomol. Soc.* 32:283–88

139. Hinton HE. 1951. Myrmecophilous Lycaenidae and other Lepidoptera—a summary. *Proc. London Entomol. Nat. Hist. Soc.* 111–75

140. Hochberg ME, Elmes GW, Thomas JA, Clarke RT. 1996. Mechanisms of local persistence in coupled host-parasitoid associations: the case model of *Maculinea rebeli* and *Ichneumon eumerus*. *Phil. Trans. R. Soc. London Ser. B* 351:1713–24

141. Hoegh-Guldberg O. 1972. Pupal sound production of some Lycaenidae. *J. Res. Lepid.* 10:127–47

142. Hölldobler BE, Wilson EO. 1990. *The Ants*. Cambridge, MA: Belknap Press Harvard Univ. 732 pp.

143. Holloway JD, Nielsen ES. 2000. Biogeography of the Lepidoptera. In *Handbook of Zoology*, ed. NP Kristensen, pp. 423–62. New York: de Gruyter

144. Howe HE. 1975. *The Butterflies of North America*. New York: Doubleday. 633 pp.

145. Jackson THE. 1937. The early stages of some African Lycaenidae (Lepidoptera), with an account of larval habits. *Trans. R. Entomol. Soc. London* 86:201–38

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

147. Johnson K, Miller LD, Herrera J. 1991. *Eiseliana* and *Heoda*, high Andean and austral genera of the Neotropical Eumaeini (Lepidoptera: Lycaenidae). *Acta Entomol. Chil.* 17:107–46

148. Johnson K, Coates S. 1999. *Nabokov's Blues: The Scientific Odyssey of a Literary Genius*. Cambridge, MA: Zoland Books. 372 pp.

149. Jordano D, Thomas CD. 1992. Specificity of an ant-lycaenid interaction. *Oecologia* 91:431–38

150. Kielland J. 1990. *Butterflies of Tanzania*. Melbourne: Hill House. 363 pp.

151. King AJ, Ring LR. 1996. The life history of *Arhopala wildei wildei* Miskin (Lepidoptera: Lycaenidae). *Aust. Entomol.* 23:117–20

152. Kitching RL. 1987. Aspects of the natural

history of the lycaenid butterfly *Allotinus major* in Sulawesi. *J. Nat. Hist.* 21:535–44

153. Kitching RL, Luke B. 1985. The myrmecophilous organs of the larvae of some British Lycaenidae (Lepidoptera): a comparative study. *J. Nat. Hist.* 19:259–76

154. Kitching RL, Taylor MFJ. 1981. The culturing of *Jalmenus evagoras* (Donovan) and its attendant ant, *Iridomyrmex anceps* (Roger). *Aust. Entomol. Mag.* 7:71–75

155. Kudrna O. 1986. *Butterflies of Europe. Aspects of the Conservation of Butterflies in Europe*, Vol. 8. Wiesbaden: Aula-Verlag. 323 pp.

156. Lahav S, Soroker V, Hefetz A, Vander Meer RK. 1999. Direct behavioral evidence for hydrocarbons as ant recognition discriminators. *Naturwissenschaften* 86:246–49

157. Lamborn WA. 1913. On the relationship between certain West African insects, especially ants, Lycaenidae and Homoptera. *Trans. Entomol. Soc. London.* pp. 436–98

158. Larsen TB. 1991. *The Butterflies of Kenya and Their Natural History*. Oxford: Oxford Univ. Press. 490 pp.

159. Layberry RA, Hall PW, Lafontaine JD. 1998. *The Butterflies of Canada*. Toronto: Univ. Tor. Press. 280 pp.

160. Leimar O, Axen AH. 1993. Strategic behaviour in an interspecific mutualism: interactions between lycaenid larvae and ants. *Anim. Behav.* 46:1177–82

161. Le Masne G. 1953. Observations sur les relations entre le couvain et les adultes chez les Fourmis. *Ann. Sci. Nat.* 15:1–56

162. Lenz F. 1917. Kleinere Mitteilungen. Der Erhaltungsgrund der Myrmekophilie. *Zeit. Induk. Abstamm. Vererbungsl.* 18:44–48

163. Lukhtanov V, Lukhtanov A. 1994. Die Tagfalter Norwestasiens (Lepidoptera, Diurna). *Herbipoliana* 3:1–440

164. Malicky H. 1969. Versuch einer Analyse der ökolgischen Beziehungen zwischen Lycaeniden (Lepidoptera) und Formiciden (Hymenoptera). *Tijdschr. Entomol.* 112:213–98

165. Malicky H. 1970. New aspects of the association between lycaenid larvae (Lycaenidae) and ants (Formicidae, Hymenoptera). *J. Lepid. Soc.* 24:190–202

166. Markl H. 1973. The evolution of stridulatory communication in ants. *Proc. 7th Int. Congr*, pp. 258–65. London: IUSSI

167. Maschwitz U, Wüst M, Schurian K. 1975. Bläulingsraupen als Zuckerlidferanten für Ameisen. *Oecologia* 18:17–21

168. Miller LD, Miller JY. 1997. Gondwanan butterflies: the Africa-South America connection. *Metamorphosis* (*Suppl.*) 3:42–45

169. Morel L, Vander Meer RK. 1988. Do ant brood pheromones exist? *Ann. Entomol. Soc. Am.* 81:705–10

170. Nabokov VV. 2000. *Nabokov's Butterflies: Unpublished and Uncollected Writings*. Boston: Beacon. 782 pp.

171. Nash DR. 1990. *Cost-benefit analysis of a mutualism between lycaenid butterflies and ants*. PhD thesis. Oxford Univ.

172. Nelson DR, Blomquist GJ. 1995. Insect waxes. In *Waxes: Chemistry*, *Molecular Biology and Functions*, ed. RJ Hamilton, W.W. Christie, pp. 1–89. Edinburgh: Oily Press

173. New TRE. 1993. *Conservation biology of Lycaenidae (butterflies)*. *Rep. 8*, Gland, Switz.: IUCN Publ. 173 pp.

174. Newcomer EJ. 1912. Some observations on the relation of ants and lycaenid caterpillars, and a description of the relational organs of the latter. *J. NY Entomol. Soc.* 20:31–36

175. Parry G, Mordan ED. 1979. Pheromones of ants: a review. *Physiol. Entomol.* 4:161–89

176. Parsons MJ. 1996. Gondwanan evolution of the Troidine swallowtails (Lepidoptera: Papilionidae): cladistic reappraisals using mainly immature stage characters, with focus on the Birdwings *Ornithoptera* Boisduval. *Bull. Kitakyushu Mus. Nat. Hist.* 15:43–118

177. Penz CM, DeVries PJ. 1999. The higher level phylogeny of the tribe Lemoniini (Lepidoptera: Riodinidae): a preliminary assessment using adult morphology. *Am. Mus. Nov.* 2384:1–32

178. Peterson MA. 1993. The nature of ant attendance and the survival of larval *Icaricia acmon* (Lycaenidae). *J. Lepid. Soc.* 47:8–16

179. Pierce NE. 1984. Amplified species diversity: a case study of an Australian lycaenid butterfly and its attendant ants. In *The Biology of Butterflies*, ed. RI Vane-Wright, PR Ackery, pp. 197–200. London: Academic

180. Pierce NE. 1985. Lycaenid butterflies and ants: selection for nitrogen fixing and other protein rich food plants. *Am. Nat.* 125:888–95

181. Pierce NE. 1987. The evolution and biogeography of associations between lycaenid butterflies and ants. In *Oxford Surveys in Evolutionary Biology*, ed. PH Harvey, L Partridge, pp. 89–116. Oxford: Oxford Univ. Press

182. Pierce NE. 1989. Butterfly-ant mutualisms. In *Toward a More Exact Ecology*, ed. PJ Grubb, JB Whittaker, pp. 299–324. Oxford: Blackwell Sci.

183. Pierce NE. 1995. Predatory and parasitic Lepidoptera: carnivores living on plants. *J. Lepid. Soc.* 49:412–53

184. Pierce NE, Easteal S. 1986. The selective advantage of attendant ants for the larvae of a lycaenid butterfly, *Glaucopsyche lygdamus*. *J. Anim. Ecol.* 55:451–62

185. Pierce NE, Elgar MA. 1985. The influence of ants on host plant selection by *Jalmenus evagoras*, a myrmecophilous lycaenid butterfly. *Behav. Ecol. Sociobiol.* 16:209–22

186. Pierce NE, Kitching RL, Buckley RC, Taylor MFJ, Benbow KR. 1987. The costs and benefits of cooperation between the Australian lycaenid butterfly, *Jalmenus evagoras*, and its attendant ants. *Behav. Ecol. Sociobiol.* 21:237–48

187. Pierce NE, Mead PS. 1981. Parasitoids as selective agents in the symbiosis between lycaenid butterfly larvae and ants. *Science* 211:1185–87

188. Pierce NE, Nash DR. 1999. The Imperial Blue: *Jalmenus evagoras* (Lycaenidae). In *The Biology of Australian Butterflies*, ed. RL Kitching, E Sheermeyer, RE Jones, NE Pierce, pp. 279–315. Sydney: CSIRO Press

189. Powell J, Mitter C, Farrell BD. 1998. Evolution of larval food preferences in Lepidoptera. In *Handbook of Zoology*, ed. NP Kristensen, pp. 403–22. New York: de Gruyter

190. Pringle ELL, Henning GA, Ball JB. 1994. *Pennington's Butterflies of Southern Africa*. Cape Town: Struik Winchester. 800 pp.

191. Rand D, Heath A, Suderman T, Pierce NE. 2000. Phylogeny and life history evolution of the genus *Chrysoritis* within the Aphnaeini (Lepidoptera: Lycaenidae), inferred from mitochondrial cytochrome oxidase I sequences. *Mol. Phylogenet. Evol.* 17:85–96

192. Robbins RK. 1991. Cost and evolution of a facultative mutualism between ants and lycaenid larvae (Lepidoptera). *Oikos* 62:363–69

193. Robbins RK. 1991. Evolution, comparative morphology, and identification of the eumaeine butterfly genus *Rekoa* Kaye (Lycaenidae: Theclinae). *Smithson. Contrib. Zool.* 498:1–64

194. Robbins RK, Venables BAB. 1991. Synopsis of a new Neotropical hairstreak genus *Janthecla* (new genus) and description of a new species (Lycaenidae). *J. Lepid. Soc.* 45:11–33

195. Rojo de la Paz A. 1990. Two new cases of myrmecophily in the Lycaenidae (Lepidoptera); biology of *Cigaritis zohra* (Donzel, 1847) and *Cigaritis allardi* (Oberthur, 1909) in Morocco. *Nota Lepid. Suppl.* 4:14–17

196. Ross GN. 1964. Life history studies on Mexican butterflies. III. Early stages of

Anatole rossi, a new myrmecophilous metalmark. *J. Res. Lepid.* 3:81–94

197. Ross GN. 1966. Life history studies on Mexican butterflies. IV. The ecology and ethology of *Anatole rossi*, a myrmecophilous metalmark (Lepidoptera: Riodinidae). *Ann. Entomol. Soc. Am.* 59:985–1004

198. Savignano DA. 1994. Benefits to Karner Blue butterfly larvae from association with ants. In *Karner Blue Butterfly: A Symbol of a Vanishing Landscape*, ed. DA Andrew, RJ Baker, CP Lane, pp. 37–46. St. Paul, MN: Minn. Agric. Exp. Sta.

199. Schlosz M, Brinkman T. 1991. The life history of *Tylopaedia sardonyx peringueyi* (Aurivillius). *J. Entomol. Soc. S. Afr.* 54:81–84

200. Schonrogge K, Wardlaw JC, Thomas JA, Elmes GW. 2000. Polymorphic growth rates in myrmecophilous insects. *Proc. R. Soc. London Ser. B* 267:771–77

201. Schurian KG, Fiedler K. 1991. Einfache Methoden zur Schwallwahrnehmung bei Bläulings-Larven (Lepidoptera: Lycaenidae). *Entomol. Z.* 101:393–412

202. Schurian KG, Fiedler K. 1994. Zur Biologie von *Polyommatus* (*Lysandra*) *dezinus* (De Freina & Witt) (Lepidoptera: Lycaenidae). *Nachr. Entomol. Verins Apollo* 14:339–53

203. Scott JA. 1986. *The Butterflies of North America*. Stanford, CA: Stanford Univ. Press. 583 pp.

204. Scott JA, Wright DM. 1990. Butterfly phylogeny and fossils. In *Butterflies of Europe*, ed. O Kudrna, pp. 152–208. Wiesbaden, Ger.: Aula

205. Seki Y, Takanami Y, Otsuka K. 1991. *Butterflies of Borneo, No. 1: Lycaenidae*. Tokyo: Tobishima Corp. 113 pp.

206. Seufert P, Fiedler K. 1996. 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. *Oecologia* 106:127–36

207. Shattuck SO. 1993. Revision of the

Iridomyrmex purpureus species-group (Hymenoptera: Formicidae). *Invertebr. Taxon.* 7:113–49

208. Shields O. 1989. World numbers of butterflies. *J. Lepid. Soc.* 43:178–83

209. Smiley JT, Atsatt PR, Pierce NE. 1988. Local distribution of the lycaenid butterfly, *Jalmenus evagoras*, in response to host ants and plants. *Oecologia* 76:416–22

210. Strong DR, Lawton JH, Southwood SR. 1984. *Insects on Plants: Community Patterns and Mechansims*. Cambridge, MA: Harvard Univ. Press. 311 pp.

211. Suderman T. 2000. *Constructing a molecular phylogeny of the Aphnaeini (Lepidoptera: Lycaenidae)*. Senior thesis. Amherst Coll., Amherst. 61 pp.

212. Thomann H. 1901. Schmetterlinge und Ameisen. Beobachtungen über einer Symbiose zwischen *Lycaena argus* L. und *Formica cinerea* Mayr. *Jaresbericht Naturforsch. Ges. Graubündens* 44:1–40

213. Thomas JA, Elmes GW. 1993. Specialized searching and the hostile use of allomones by a parasitoid whose host, the butterfly *Maculinea rebeli*, inhabits ant nests. *Anim. Behav.* 45:593–602

214. Thomas JA, Elmes GW. 1998. Higher productivity at the cost of increased host-specificity when *Maculinea* butterfly larvae exploit ant colonies through trophallaxis rather than by predation. *Ecol. Entomol.* 23:457–64

215. Thomas JA, Elmes GW. 2001. Food-plant niche selection rather than the presence of ant nests explains oviposition patterns in the myrmecophilous butterfly genus *Maculinea. Proc. R. Soc. London Ser. B* 268:471–77

216. Thomas JA, Elmes GW, Wardlaw JC. 1998. Polymorphic growth in larvae of the butterfly *Maculinea rebeli*, a social parasite of *Myrmica* ant colonies. *Proc. R. Soc. London Ser. B* 265:1895–901

217. Thomas JA, Elmes GW, Wardlaw JC, Woyciechowski M. 1989. Host specificity among *Maculinea* butterflies in *Myrmica* ant nests. *Oecologia* 79:452–57

218. Thomas JA, Simcox DJ, Wardlaw JC, Elmes GW, Hochberg ME, Clarke RT. 1998. Effects of latitude, altitude and climate on the habitat and conservation of the endangered butterfly *Maculinea arion* and its *Myrmica* ant hosts. *J. Insect Conserv.* 2:39–46

219. Thomas JA, Wardlaw JC. 1990. The effect of queen ants on the survival of *Maculinea arion* larvae in *Myrmica* ant nests. *Oecologia* 85:87–91

220. Thomas JA, Wardlaw JC. 1992. The capacity of a *Myrmica* ant nest to support a predacious species of *Maculinea* butterfly. *Oecologia* 91:101–9

221. Thomas ML, Parry LJ, Allan RA, Elgar MA. 1999. Geographic affinity, cuticular hydrocarbons and colony recognition in the Australian meat ant *Iridomyrmex purpureus. Naturwissenschaften* 86:87–92

222. Travassos MA, Pierce NE. 2000. Acoustics, context and function of vibrational signalling in a lycaenid butterfly-ant mutualism. *Anim. Behav.* 60:13–26

223. Uchida H. 1995. *The Beautiful Butterfly Island Formosa Forever* (in Japanese). Tokyo: Shinwa. 208 pp.

224. Vander Meer RK, Morel L. 1988. Brood pheromones in ants. In *Advances in Myrmecology*, ed. JC Trager, pp. 491–513. Leiden, The Netherlands: Brill

225. Van Dyck H, Oostermeijer H, Talloen JGB, Feenstra V, Van der Hidde A, Wynhoff I. 2000. Does the presence of ants matter for oviposition to a specialized myrmecophilous *Maculinea* butterfly? *Proc. R. Soc. London Ser. B* 267:861–66

226. Vane-Wright RI. 1978. Ecological and behavioural origins of diversity in butterflies. In *Diversity of Insect Faunas*, ed. LA Waloff, R Waloff, pp. 56–69. New York: Blackwell Sci. Publ.

227. Völkl W, Woodring J, Fischer M, Lorenz MW, Hoffmann KH. 1999. Ant-aphid mutualisms: the impact of honeydew production and honeydew sugar composition on ant preferences. *Oecologia* 118:483–91

228. Wada A, Isobe Y, Yamaguchi S, Yamaoka R, Ozaki M. 2001. Taste-enhancing effects of glycine on the sweetness of glucose: a gustatory aspect of symbiosis between the ant, *Camponotus japonicus* and the larvae of the lycaenid butterfly, *Niphanda fusca. Chemical Senses.* In press

229. Wagner D. 1993. Species-specific effects of tending ants on the development of lycaenid butterfly larvae. *Oecologia* 96:276–81

230. Wagner D. 1994. *Species-specific effects of tending ants on the life history of Hemiargus isola, a North American lycaenid butterfly*. PhD thesis. Princeton Univ. 121 pp.

231. Wagner D. 1995. Pupation site choice of a North American lycaenid butterfly: the benefits of entering ant nests. *Ecol. Entomol.* 20:384–92

232. Wagner D, Kurina L. 1997. The influence of ants and water availability on oviposition behavior and survivorship of a facultatively ant-tended herbivore. *Ecol. Entomol.* 22:352–60

233. Wagner D, Martinez del Rio C. 1997. Experimental tests of the mechanism for ant-enhanced growth in an ant-tended lycaenid butterfly. *Oecologia* 112:424–29

234. Walsh JP, Tschinkel WR. 1974. Brood recognition by contact pheromone in the red imported fire ant, *Solenopsis invicta. Anim. Behav.* 22:695–704

235. Wardlaw JC, Thomas JA, Elmes GW. 2000. Do *Maculinea rebeli* caterpillars provide vestigial mutualistic benefits to ants when living as social parasites inside *Myrmica* ant nests? *Entomol. Exp. Appl.* 95:97–103

236. Weidemann HJ. 1995. *Tagfalter—Biologie, Ökologie, Biotopschutz*. Augsburg: Naturbuch. 659 pp.

237. Westoby M, Rice B, Shelley JM, Haig D, Kohen JL. 1982. Plants' use of ant dispersal at West Head, New South Wales.

In *Ant-Plant Interactions in Australia*, ed. RC Buckley, pp. 75–89. The Hague: Junk

238. Wiemers M. 1995. The butterflies of the Canary Islands: a survey on their distribution, biology and ecology (Lepidoptera: Papilionoidea and Hesperioidea). *Linn. Belgica* 15:63–84; 7–118

239. Williams MC. 1990. Observations of the biology of *Lepidochrysops plebeia plebeia* (Butler) (Lycaenidae: Polyommatinae). *Metamorphosis* 1:10–11

240. Wilson EO. 1971. *The Insect Societies*. Cambridge, MA: Belknap Press Harvard Univ. Press