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PAUL H. HARVEY AND LINDA PARTRIDGE

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The evolution and biogeography of associations between lycaenid butterflies and ants

NAOMI E. PIERCE

Introduction

Many organisms make a living from scratching each other's backs, and many survive at the expense of others. Once a complex interaction has arisen between two organisms, what effect can such a relationship have on their subsequent evolution? This paper will consider the evolutionary consequences of associations among lycaenid butterflies, their host plants, ants, parasitoids, and predators. The Lycaenidae are especially interesting from an ecological and evolutionary perspective because they exhibit dramatic variety in their life histories. The larvae of many species associate with ants, and these relationships can be parasitic, commensal, or mutualistic. Larvae can be carnivorous or herbivorous; and some species interact with many species of ants, whereas others are species-specific. It is partly because of this complexity and diversity that the Lycaenidae have not been studied as intensively as other butterfly families, and I will discuss at least three problems that have hampered our understanding of their ecology and evolution. In particular, more must be learned about the nature of the exocrine secretions of lycaenid larvae, and whether they function to reward, appease, and/or deceive their associated ants. The association between lycaenids and ants has had several important evolutionary consequences, and I will show how these relate to the question of why there are so many species of lycaenid butterflies. Finally, I will discuss an unresolved pattern in the biogeography of lycaenid butterflies: association with ants in general, and species-specific interactions in particular, are far more common among lycaenids found in Ethiopian, Oriental, and Australasian regions than among those from the Holarctic.

Natural history: from parasitism to mutualism

The larvae of at least nine families in the Lepidoptera associate with ants, and of these, the overwhelming majority are in the Lycaenidae (Hinton 1951; Maschwitz *et al.* 1986). Lycaenid caterpillars have at least three kinds of exocrine glands that secrete substances to attract and/or communicate with ants, and these form the basis of their myrmecophilous relationships. The larvae of all lycaenids that have been examined possess one of these ant-associated structures: epidermal glands called 'pore cupolas' are scattered over their surfaces and concentrated in regions that commonly elicit palpation by ants.

of homopterans, and a number actually prey on the homopterans themselves (see Hinton 1951; Kitching 1987; Maschwitz *et al.* 1985). It is thought that the latter evolved sequentially via a form that initially harvested the honeydew of sap-feeding insects, especially aphids (Fukuda *et al.* 1978; Cottrell 1984). Again Japan has an excellent example in the form of *Taraka hamada*, whose larvae prey primarily on the aphid *Ceratovacuna japonica* (Fukuda *et al.* 1984). This aphid species is known to possess a 'soldier caste' of specialized first instar nymphs, which defend the aphid colony against predators (cf. Aoki *et al.* 1981, 1984). These soldiers do not moult, but eventually die without ever producing progeny. The larvae of *T. hamada* are well adapted to feeding on colonies of *C. japonica*: the vulnerable early instars weave a silken tent in which they hide, emerging only to seize passing aphids and drag them back into their lairs. If this protection is removed, single soldier aphids are sufficiently powerful to kill a first instar caterpillar (N. E. Pierce, personal observation). The importance of this aphid in the life history of *T. hamada* is reinforced by the activity of the adults, which, rather than feeding on flower nectar, as most butterflies do, spend long hours feeding on the honeydew produced by the same species of aphid. Thus, every phase of the life cycle of *T. hamada* is centred around *C. japonica.*

Associations between the larvae of herbivorous lycaenids and ants are much more common than the parasitic and carnivorous relationships discussed above. Some of these relationships appear to be good examples of commensalism. For example, the larvae of *Deloneura ochrascens* are found with ants of the species *Crematogaster castenea* among lichens on tree bark (*Acacia stenocarpus*) (Jackson 1937). The larvae feed on the lichen, and do not interact behaviourally with the ants. Nevertheless, larvae often nestle in the entrances of the ant galleries, and probably gain protection from their proximity to ants. Other African species such as *Iridana incredibilis* and *Iridana perdita* have similar life histories (Jackson 1937).

While these examples suggest that some lycaenids benefit indirectly from their proximity to ants, the larvae of other herbivorous lycaenids benefit quite directly from ant attendance. Experiments have shown for a number of these species that ants protect the caterpillars against predators and parasitoids (e.g. Ross 1966; Pierce and Mead 1981; Pierce and Easteal 1986; Pierce *et al.* 1987). From the point of view of the lycaenids, the strength of the interaction may range from being loosely facultative to strictly obligate, depending on the species involved. Most of the species in the Nearctic fall into the 'loosely facultative' category, because the caterpillars are not tended continuously and may associate with as many as a dozen species of ants (cf. Downey 1962b). For example, field experiments on *Glaucopsyche lygdamus* in Colorado showed that the presence of ants significantly reduced the attack of larvae by parasitoids, but that a small number of larvae survived to pupate even in the absence of ants (Pierce and Easteal 1986). An 'obligate' association, on the other hand, is typically one in which lycaenid larvae are never found without attendant ants, and are often found with only one species or genus of ant. For example, larvae of the Australian lycaenid *Ogyris genoveva* associate exclusively with a species of *Camponotus.* The caterpillars of *O. genoveva* feed at night (when the risks of predation and parasitism may be relatively low) on mistletoes that parasitize *Eucalyptus* trees; during the day the caterpillars can be found with ants in shallow galleries excavated by the ants at the base of the tree. At dawn, the ants guide the larvae off the mistletoe down to the safety of the galleries at the tree base, and at dusk they herd them up the tree to their feeding sites (Common and Waterhouse 1981).

The Australian lycaenid *Jalmenus evagoras* is another example of a lycaenid whose larvae are obligately dependent upon an attendant ant guard, and in this case the relationship has been shown to be a truly mutualistic one. Four ant-exclusion experiments in three field sites demonstrated that predation and parasitism of the larvae and pupae of this butterfly are so intense that individuals deprived of their attendant ant, *Iridomyrmex anceps*, cannot survive (Pierce *et al.* 1987). Not surprisingly, females of *J. evagoras* use this ant species as a cue in oviposition (Pierce and Elgar 1985). In return for tending and protecting the larvae, ants are rewarded by food secretions that are rich in free amino acids, particularly serine (Pierce *et al.* 1987; Pierce *et al.*, in preparation). These rewards are produced at a metabolic cost to the lycaenids: laboratory experiments demonstrated that larvae that are tended by ants pupate at a significantly lower weight than larvae that are not tended, and that the adults emerging from these pupae are also lighter and smaller (Pierce *et al.* 1987). This constitutes a significant cost to the butterfly, as relative size is an important determinant of lifetime mating success in males of *J. evagoras*, and absolute weight is an important determinant of fecundity in females (Elgar and Pierce 1987).

Like many other lycaenids that have close associations with ants (Kitching 1981), females of *J. evagoras* lay their eggs in clusters, and the larvae and pupae aggregate. If a threshold number of ants is necessary to protect the larvae and pupae, then aggregating is one mechanism by which *J. evagoras* could simultaneously increase its collective defence and decrease the amount of food that each individual would need to produce to attract that defence. For example, field observations of a population of *J. evagoras* showed that first instar larvae gained more ants by joining a group of any size than by remaining alone, and that second or third instars had a higher number of attendant ants when they joined a mean-sized group of about four larvae than they did when they foraged alone (Pierce *et al.* 1987). Moreover, aggregation is not entirely automatic, but occurs, at least in part, in response to ants: young instars that are not tended by ants are less likely to form groups than their tended counterparts (Pierce *et al.* 1987).

Facultative associations between lycaenids and ants are not usually characterized by species specificity. For example, the North American species *Glaucopsyche lygdamus* is tended by at least six different species of ants

(Pierce and Mead 1981). This suggests that the food reward and/or form of chemical communication produced by the caterpillars of these lycaenids is generally attractive to a whole range of ant species. On the other hand, parasitic lycaenids that chemically trick their host-ant species to gain entry to the nest must produce specialized attractants that both appease the host-ant aggression and cause the ants to carry the lycaenid larvae into the ant nest. Parasitic lycaenids are almost always host-specific, although occasional 'mistakes' have been recorded. The late instar larvae of *Maculinia telius*, a Japanese species that normally parasitizes the ant *Myrmica ruginoides*, were once discovered in the nest of a colony of *Lasius niger* (Fukuda *et al.* 1978). Species or genus specificity is also common among herbivorous lycaenids that have obligate associations with ants: for example, *J. evagoras* associates with only a few species of ants in the genus *Iridomyrmex*. A more extreme case of this kind of specificity is shown by *Hypochrysops ignitus*, an Australian lycaenid whose larvae feed on at least seventeen different plant families, but associate exclusively with a single species of ant, *Iridomyrmex nitidus* (Common and Waterhouse 1981). If the larva of a species-specific lycaenid is placed in contact with an unfamiliar ant species, the ants often attack and kill it. Thus, in species-specific associations, communication between the caterpillars and the ants is clearly involved: the parasitic lycaenid must fool its host ant species into thinking that it is something it is not (such as a 'desirable guest'), and a species-specific, herbivorous lycaenid must persuade only the appropriate ants to tend it all the time.

Three difficulties

Although they comprise perhaps 40 per cent of all butterfly species (Vane Wright 1978), the Lycaenidae are a surprisingly poorly understood group. There are at least three difficulties that have contributed to this lack of understanding: the first two are essentially historical and logistical, but the third stems in part from a misconception about the relationship between lycaenids and ants. First, the lycaenids are known to feed on a bewildering array of food plants, including such diverse taxa as lichens, mistletoes, bamboos, oaks, ferns, conifers, and cycads (see Atsatt 1981b). In their influential paper, Ehrlich and Raven (1964) pointed out that no phytochemical common denominator seemed to underlie this diverse range of host plants, and they concluded that the Lycaenidae were unlikely to be an amenable subject for the study of the broad effects of insect–plant coevolution. Nevertheless, Downey (1962a) drew attention to the preponderance of legume-feeders amongst the lycaenids; Breedlove and Ehrlich (1968) and Dolinger *et al.* (1973) investigated chemical aspects of the relationship between *Glaucopsyche lygdamus* and its food plants; and Cottrell (1985) mentioned the possibility of coevolution of the genus *Capys* with its host plants. In general, however, the lycaenids have been overlooked in the spate of careful experimental analysis that followed Ehrlich and Raven's paper; these studies had focused on other butterfly groups such as the Papilionidae (e.g. Ehrlich and Raven 1964; Feeny 1975; Berenbaum and Feeny 1981; Berenbaum 1981, 1983; Rauscher and Feeny 1980), the Pieridae (e.g. Chew 1975; Chew and Rodman 1979; Rodman and Chew 1980), the Danaines (e.g. Brower and Brower 1964), and the Heliconiines (e.g. Gilbert 1971, 1982, 1983).

A second difficulty that has hampered evolutionary studies of the Lycaenidae stems from the failure of many collectors and naturalists to appreciate the importance of ant associations in the biology of these butterflies. This neglect is easily explained by lack of familiarity. Information about ant association (such as species identifications) is notably poor in geographic regions such as North America, where interactions with ants are primarily facultative, loose associations. In contrast, in regions such as Australia where ant associations are more common and often species-specific, the literature is correspondingly more complete (e.g. Common and Waterhouse 1981). The unfortunate consequence of the irregular documentation of lycaenid–ant associations is that it is hard to piece together a comprehensive picture of the distribution of these associations throughout the family, and such information is of critical importance to our understanding of the ecology and evolution of the group.

Finally, a hindrance to the progress of research into lycaenid–ant interactions comes from the analogy often made between myrmecophily in the Lycaenidae and in the Homoptera. References to the 'honeydew' or 'nectar' glands of the Lycaenidae are common (but see Malicky 1969, 1970; Maschwitz *et al.* 1975, who clearly delineate this problem). Until recently, the only study of the secretions of the dorsal organ of a lycaenid was on those of *Lysandra hispana* (Maschwitz *et al.* 1975), which demonstrated that they contained sucrose, fructose, glucose, and trehalose in concentrations of 13–19 per cent, and trace amounts of the amino acid methionine. The apparent predominance of carbohydrates in the secretions of *L. hispana* supported the notion that the secretions of the Lycaenidae are essentially similar to those of the Homoptera, and lycaenids have accordingly been lumped together with homopterans and extra-floral nectaries in treatments of their ecological associations with ants (cf. Atsatt 1981b; Buckley 1982; Beattie 1985). It is entirely likely that the dorsal organs of many lycaenids do in fact function analogously to honeydew glands and nectaries of other kinds (Horvitz and Schemske 1984; Maschwitz *et al.* 1984); but treating them in this way ignores an important feature: namely, that the secretions of the Lycaenidae derive from specialized exocrine glands and are not an egestion, as is the honeydew of homopterans.

The degree of control that lycaenid larvae have over their secretions places them more appropriately among myrmecophiles that maintain relations with ants, usually by chemical mimicry of some sort (as noted by Wilson 1971), than among trophobionts such as homopterans. Aphids and membracids produce honeydew whether or not ants are there to tend them. Of course, selection on this system has favoured the evolution of many specialized ant adaptations by aphids and membracids, such as morphological structures with which to hold and offer droplets of honeydew (Way 1963), chemical modification of certain components of the honeydew (Gray 1952; Strong 1965; Auclair 1963), allomones that mimic ant alarm signals (Nault *et al.* 1976), and behavioural adaptations to take full advantage of ant protection (Bristow 1983). But the ant rewards produced by homopterans are essentially waste materials, whereas those produced by lycaenids are manufactured specifically for ants.

Parasitic and species-specific interactions provide evidence that lycaenids can manipulate the behaviour of their attendant ants, and thus care must be taken in interpreting relationships that may initially appear to be mutualistic. For example, larvae of the North American species *Glaucopsyche lygdamus* that are tended by workers of *Formica altipetens* are far more likely to survive to eclosion than their untended counterparts, and ants can be seen to forage regularly on the dorsal organ secretions of the third and fourth instars of this butterfly (Pierce and Easteal 1986). Taken together, these observations suggest that the relationship is mutualistic. However, more must be learned about the nature of these rewards before making such a claim. For example, if rewards provided for ants are produced at a metabolic cost to larvae, selection would favour any individual that could attract protection from attendants at the least possible cost. And if the cost of producing substances to fool ants into providing protection is cheaper metabolically than the cost of producing substances to reward ants, then selection would favour parasitism. Maschwitz *et al.* (1975) approached this problem by estimating the number of droplets secreted by a late instar larva of *Lysandra hispana* feeding on *Hippocrepis comosa* (Fabaceae). When tended by hungry workers of *Lasius flavus*, the larva could produce as many as 51 droplets in 1 hour. Since these secretions were approximately 13–19 per cent carbohydrate, there seems little doubt that the ants were receiving considerable rewards from the larvae of this species, and that the relationship in this case was therefore mutualistic (see also Degen *et al.* 1986).

A conceptual framework

Several factors may have influenced the evolution of complex associations between lycaenid butterflies and ants. Both taxa are holometabolous, and thus different stages of the life history are specialized to carry out different functions. Specialization in one aspect may lead to constraint in another. Caterpillars are adapted primarily for feeding on plants, and in general rely for defence on passive mechanisms such as aposematism, crypsis, concealment, or, in this case, attracting ants. Agricultural ants such as species of *Iridomyrmex* that tend nectaries and honeydew-producing insects are likewise well equipped for foraging, but in a manner that includes an elaborate and active defence system. These specializations mean that the benefit derived by each species from its partner is qualitatively different (see Pierce and Young 1986).

Both partners in a lycaenid–ant interaction can control the amount of benefit that they provide. Co-operation by the ants takes the form of defence that can vary, depending upon the context. For example, the ants could provide only enough protection to optimize their immediate energetic gains. Alternatively, they may provide a surplus of defence if it maximizes the population growth of their lycaenid associates and hence the long-term, net gains of the colony. The latter possibility seems likely in relationships such as the one between *Jalmenus evagoras* and *Iridomyrmex anceps*: the ants do not attack and eat the vulnerable pre-pupae or freshly eclosed adults, as might be predicted if they were simply maximizing their immediate energy gain. Similarly, a lycaenid that co-operates by secreting food for ants is able to vary both the quality and the quantity of the reward. As described before, this possibility exists because the secretions provided by individual lycaenids for ants are derived from exocrine glands that are under the lycaenid's control (but see Hinton 1951 for one or two possible exceptions).

The qualitative differences in benefits derived by lycaenids and ants have influenced the evolutionary options available for each species, and it is useful to consider these in the context of game theory (e.g. Axelrod and Hamilton 1981; Maynard Smith 1982), in part because it suggests directions for further research. In particular, I can think of three kinds of interactions between lycaenids and ants that may initially appear to be mutualistic; but upon closer examination, only one of these is an example of reciprocal co-operation (Trivers 1971). These interactions are determined by the nature of the secretions produced by the lycaenids, and in the discussion of the evolution of these secretions, I follow the terminology of Holldobler (1970, 1971, 1978), who first described what appears to be an analogous set of secretions produced by the aleochocrine staphylinid beetles in gaining acceptance by their host ants. The first case describes the condition which I consider to be ancestral simply because it is the easiest pathway by which to imagine lycaenid–ant co-operation arising. This scenario is also in accord with the generally held opinion that early lycaenids were myrmecophilous (Hinton 1951; Malicky 1969; Fukuda *et al.* 1978). The first case might have then been followed by the latter two cases, both of which describe the kinds of associations found between species of lycaenids and ants today.

1. REWARD ONLY: FARMING OF LYCAENIDS BY ANTS

Consider a situation in which a lycaenid larva produces a secretion, perhaps a nutritious drop of haemolymph, that serves as food for marauding ants. This secretion (or 'appeasement substance'; Holldobler 1971) would not necessarily mimic an ant chemical communication signal, but would merely contain a food that the ants like to collect, thereby diverting them sufficiently for the lycaenid to escape attack. In this case, lycaenids co-operate with ants by secreting this food, and in return, ants might eventually co-operate with lycaenids by tending and protecting them. However, if an individual lycaenid does not secrete enough food, its ants will respond by eating it. Clearly, an evolutionary game of this sort would be truncated whenever an ant colony chose not to co-operate, but to defect by eating the lycaenid. Note that it would be impossible for a lycaenid to retaliate if its ant colony defected against it. The 'co-operation' exhibited by the lycaenids and ants would reflect farming on the part of the ants. An ant colony could use the decision rule: tend a lycaenid only as long as its food rewards exceed a threshold cost of tending (determined by the energy required to collect secretions and defend), otherwise cease tending and attack. A complicating feature of this decision is that the lycaenids represent a renewable resource, and thus the ant colony could ideally have some means by which to assess long-term net gains from a lycaenid, both in itself and in its offspring, and weigh them against the immediate gain from eating that lycaenid. In this situation, selection would favour any characteristic that would enable a lycaenid to defend itself against its attendant ants, and this might have led to the evolution of the control and reward conditions described below.

2. ANT CONTROL AND REWARD: TRUE CO-OPERATION BETWEEN LYCAENIDS AND ANTS

Suppose that in addition to providing food for ants such as carbohydrates and amino acids, lycaenids secrete substances that cause ants always to treat them in a friendly manner. These substances might be allomones that mimic ant communication signals: Holldobler (1970, 1971, 1978) first suggested the possibility of such secretions when he described the pseudopheromones used by *Atemeles* staphylinid beetles to gain acceptance by their host ants. In this situation, the only way an ant colony could defect against a lycaenid would be by harvesting its food rewards without defending it; the ants could not also attack and eat it. Thus, if an ant colony chose to defect, a lycaenid could retaliate by not providing significant amounts of food, while still producing the necessary secretions to protect itself from ant aggression. There is little doubt that many lycaenids can secrete substances that control ant aggression, although little is known of their chemical nature (see Henning 1983b). As mentioned before, in addition to chemical control, lycaenids are defended against ants by their unusually thick and specially contoured cuticles (Malicky 1970; see also Cottrell 1984).

If lycaenids are thus protected against ant aggression, conditions would have been met for lycaenids and ants to engage in a game that resembles an Iterated Prisoner's Dilemma game (see Axelrod and Hamilton 1981). This game captures the essence of the problem of achieving mutual co-operation: if only one partner chooses to defect rather than co-operate, it gains a higher pay-off in terms of fitness than if it co-operates; however, if both partners defect, both do worse than if they had co-operated. The following essential features are shown by lycaenid–ant interactions:

(1) There are repeated interactions, in each of which, considered on its own, each player would do better by defecting. Specifically, the ants would save labour by not defending the lycaenids, while the lycaenids could grow bigger by not feeding the ants.

(2) The players co-operate in each game because of the influence of the strategy played in one game on the opponent's play in future games. Specifically, if the ants do not defend, the lycaenids will stop feeding them; and if the lycaenids stop feeding the ants, the ants will cease defending them.

However, lycaenid–ant interactions may differ from the classical Iterated Prisoner's Dilemma game in several important ways. For example, the rewards reaped by each player are asymmetrical, and the games played between individuals are finite; thus one might expect them to change over time. That is, special circumstances may apply to situations where the interaction approaches termination, such as in the final stages of the larval and pupal life of the lycaenid, or in situations where the ant colony moves location. In both cases, the future strategy of the opponent becomes unimportant. Furthermore, in many lycaenid–ant interactions, the options of the lycaenids are limited not by the aggression of ants (since secretions may be used to pacify ants in the manner described in (2) above), but by the apparent loss of alternative means of defence against predators and parasitoids. In these situations, one reason why ants might continue to co-operate and defend lycaenids is because if they didn't, the larvae and pupae would fall prey to parasitoids and predators. This differs from the interaction outlined for the Iterated Prisoner's Dilemma in that the behaviour of the ants is not necessarily governed by their response to a strategic decision on the part of the lycaenids (i.e. to reduce the food provided for ants), but is also influenced by their response to a third party—the parasitoids and predators. Interestingly, butterflies such as *Jalmenus evagoras* possess a mechanism that reduces the possibility that they would ever associate with an ant colony that is not likely to co-operate: ovipositing females of *J. evagoras* respond to the density of conspecific larvae and ants, and lay fewer egg masses on trees containing a small number of larvae and ants than on trees with many larvae and ants (Pierce and Elgar 1985; N. E. Pierce, unpublished results).

Another complication in considering reciprocal co-operation between certain lycaenids and ants arises from the interaction that the butterflies have with each other in those species where the larvae and pupae aggregate. What are the consequences for an individual larva that defects by not secreting food rewards for the ants? If it stays in a group and takes advantage of its conspecifics, then it might still be able to reap the benefits of ant defence without paying a price. It is possible that larvae differentially aggregate into kin groups, but a defecting larva could still employ a two-part strategy of defecting and also aggregating with non-kin. This could result in a mixed Evolutionarily Stable Strategy (Maynard Smith 1982) in which the ratio of defecting to co-operating individuals is governed in a frequency-dependent fashion by the effectiveness of the ant guard and the predation and parasitism pressure of the environment, and would be qualitatively similar to a game of vigilance (Parker and Hammerstein 1985). More must be learned about the secretions of individual larvae and their behaviours before this possibility can be confirmed or refuted.

Axelrod and Hamilton (1981) have demonstrated that, provided the individuals that interact in an Iterated Prisoner's Dilemma game have a sufficiently high probability of meeting again, an evolutionarily stable strategy for each to use is tit for tat:—that is, co-operate on the first move, and thereafter do whatever the other player did on the preceding move (but see Boyd and Lorberbaum 1987). Repeated interaction between partners is an important precondition for this strategy, and while complex behaviour such as individual recognition is probably not possible for lycaenids and ants, several features of their biology would ensure the continuous interactions between participants necessary for tit for tat: the ants that associate with lycaenids maintain stable nest sites over long periods of time; the host plants of many species are perennial and reasonably large; and each larva is able to complete its development in a fixed location attended by a single ant colony. There are two difficulties, however. The first again concerns the problem of the finite nature of the interaction: each game terminates when the lycaenid undergoes metamorphosis. Secondly, while a lycaenid may interact for its entire life with only one ant colony (and thus not need to be able to distinguish it from other individuals), it is unclear whether an ant colony could identify an individual lycaenid.

3. ANT DECEPTION: PARASITISM OF ANTS BY LYCAENIDS

Finally, consider a lycaenid that produces a secretion that does not simply control ant aggression, but manipulates ant behaviour in a way that is entirely advantageous to the lycaenids. Ants could not defect in this situation, since they are being chemically fooled. A number of myrmecophiles parasitize ants in this way by producing 'adoption substances' that cause them to be carried into the ant nest (Holldobler 1978; see also Wilson 1971 for a review). As described before, the larvae of parasitic lycaenids such as *Maculinea arion* mimic the recognition signals of an ant brood, and are carried by ants into the nest, where they become carnivorous and feed on the brood. Furthermore, lycaenids that appear to have facultative and mutualistic associations with ants may actually be parasitizing them if the secretions they produce attract and maintain attendant ants without rewarding them. In these situations, selection should favour ants capable of recognizing the lycaenids' deception: the ants and lycaenids are involved in an evolutionary arms race.

Evolutionary consequences

While it is fairly straightforward to assess the proximate costs and benefits of ant association for particular species of Lycaenidae, the evolutionary ramifications that such complex relationships may have are more diffuse and difficult to identify. The main premiss, which I have suggested elsewhere (Pierce 1984) and develop more fully here, is simply that the ant-associated habits of the Lycaenidae have served to amplify the diversification of this group beyond the usual host-plant-based level found in other butterfly families. For example, behavioural adaptations of ant-tended lycaenids may lead to an expansion of host-plant range or to a higher incidence of host-plant switching. Furthermore, lycaenids with ant associations have the opportunity of becoming ant generalists or ant specialists, of losing their ant associations, or of switching ant species. The combined effects of plant and ant switching may lead to greater opportunities for subsequent diversification. Associations with ants may also limit the diversity of possible host-plant taxa that are suitable for myrmecophilous lycaenids, and ant dependence may restrict the distribution of lycaenids to those areas where appropriate host plants and ants coincide. The patchiness of overlapping resources may serve to increase population subdivision and decrease deme size, thereby possibly increasing rates of speciation.

Ant-dependent oviposition has been recorded for a number of different species of Lycaenidae (reviewed in Pierce and Elgar 1985), and as early as 1915, Bell (1915–20) suggested that an ecological and evolutionary consequence of this behaviour might be that ant-tended lycaenids possess a wider range of host plants than their untended counterparts (see also Gilbert and Singer 1975; Atsatt 1981a,b; Vane Wright 1978; Cottrell 1984). The rationale for this argument is that lycaenids that use ants as well as plants as cues in oviposition may be more likely to lay eggs on plants other than the customary host plant if the appropriate ant occurs on a novel plant. Even if the success rate of these oviposition 'mistakes' (Chew and Robbins 1984) is as low for lycaenids as it is for other species of butterflies, the absolute number of successes would be greater over evolutionary time simply because lycaenids that lay eggs in response to ants as well as plants would be likely to make mistakes more often. Accordingly, plants may have been selected for their proximity to ant nests or their attractiveness to ants. In support of this hypothesis, a comparative study of the host-plant ranges of 282 species of lycaenids that do and do not associate with ants showed that, in general, ant-tended lycaenids feed on a greater number of host-plant species, genera, and families than their untended counterparts (Pierce and Elgar 1985).

But while individual species may feed on a greater number of plant taxa, as a group, the ant-tended lycaenids do not necessarily feed on a greater diversity of plants. In general, the host plants of ant-tended lycaenids are legumes and other nitrogen-fixing plants, and lycaenids are also well known for eating nitrogen-rich parts of plants such as flowers, seed pods, and terminal foliage (Mattson 1980; see also Robbins and Aiello 1982). This pattern of host-plant use may again result from ant-associated habits. Lycaenids such as *Jalmenus evagoras* that secrete amino acids in addition to carbohydrates for attendant ants are under the double nutritional burden of securing enough protein for their own development as well as additional protein to feed their attendant ants. Thus, one might expect selection to have favoured individuals that feed on plants that are particularly rich in protein. In this context, nitrogen-fixing plants might be considered to be protein-rich for two reasons. First, both the seeds and the leaves have been recorded to contain high levels of protein relative to other plant taxa (Van Etten *et al.* 1963, 1967; Akeson and Stahman 1966). Secondly, plants that fix nitrogen may experience less temporal variation in their protein content than plants that require nitrogen sources in the soil and are therefore more vulnerable to local fluctuation. An analysis of 297 species of Lycaenidae (for which comprehensive life-history and host-plant data are available) from Australia, South Africa, and North America supported the hypothesis that ant association influences host-plant choice: myrmecophily was highly significantly associated with the consumption of nitrogen-fixing host plants (Pierce 1985).

The strong association between ant attendance and the selection of protein-rich food plants is consistent with the notion that, on the whole, ant-tended, herbivorous lycaenids interact mutualistically with their ant associates. It is possible, of course, that these lycaenids require protein in order to produce substances that fool ants chemically; but given the large amounts of food secreted for ants by larvae of species such as *Jalmenus evagoras* (Pierce *et al.* 1987), it seems reasonable that at least some myrmecophilous lycaenids need protein-rich resources to produce adequate amino acid-rich food rewards for ants. A comparison of the secretions of *Lysandra hispana* (Maschwitz *et al.* 1975) and *Jalmenus evagoras* (Pierce *et al.* 1987; Pierce *et al.*, in preparation) indicates that different species may vary greatly in the nature of the rewards they offer; but it is not surprising that the more obligate the relationship becomes from the point of view of a lycaenid that associates mutualistically with ants, the more valuable and energetically expensive its secretion. Furthermore, if the main currency of exchange between a lycaenid and its attendant ants is dietary, presumably lycaenids that need to attract ants are in competition with other food sources available to the ants. Thus, one of the selective forces that will determine the quality of the lycaenid's secretion (such as the composition and concentration of amino acids) is the quality of other resources, and these are likely to vary between habitats and geographic regions.

A great number of exceptions exist to the pattern of host-plant use described here, and features of plants other than their protein content have undoubtedly been important in shaping the host-plant choices of ant-tended lycaenids. For example, one of the main exceptions within the Australian fauna are lycaenids that feed on mistletoe: mistletoe-feeders, mostly species of *Ogyris*, usually also associate with ants. It is possible that mistletoes function in a manner similar to nitrogen-fixing plants in the sense that they can draw nitrogen up from their hosts (see discussion in Pierce 1985). However, other exceptions do not lend themselves to simple explanations. For example, the lycaenid larvae that associate with 'weaver' ants, *Oecophylla smaragdina* and *Oecophylla longinoda*, feed on a diverse array of tropical species that rarely include legumes (cf. Clark and Dickson 1971; Common and Waterhouse 1981). In these species, the food plants of the butterflies are also the host plants of the ants, as weaver ants sew their nests out of the leaves of plants. It would be interesting to know more about the chemical nature of the secretions of the larvae tended by these ants, as they may well contain compounds other than amino acids. Wilson (1987) found flavenoids in the wings and the body of *Lysandra coridon* and a number of other species, and suggested that either the distasteful aspect of these compounds or their bactericidal or antimycotic properties may have influenced ant relationships in the Lycaenidae. Robbins and Aiello (1982) noted that the flower-feeding habits of many Lycaenidae may be an adaptation that allows them to consume a wide variety of different plant taxa. Both Malicky (1969) and Atsatt (1981b) pointed out that the life habit of particular plants may influence the distribution of ants on these plants, which in turn may influence lycaenid host-plant choice. Atsatt argued that 'apparent' plants (woody perennials) are more likely to be frequented by ants than non-apparent plants, and are therefore more likely to be eaten by myrmecophilous lycaenids that seek ant-derived 'enemy free space'.

In addition to specific host-plant associations, many lycaenids maintain specific ant associations. For these lycaenids, such as species of *Jalmenus*, a shift in ant association may be as dramatic an ecological shift as a shift in host plant; thus ant shifts may also drive diversification. Moreover, depending upon selection pressures, lycaenids may become either ant specialists or ant generalists, or they may lose their ant-associated habits altogether and find other ways to protect themselves against predators and parasitoids. For example, the larvae of many species that feed in concealed locations, such as inside fruits or seed pods, are not associated with ants; others are exceedingly cryptic and often have colour polymorphisms (cf. Sibatani 1984); and some, such as the larvae of species of *Eumaeus*, that feed on cycads, are aposematically coloured and almost certainly distasteful.

If we accept that ancestral lycaenids were all myrmecophilous (Hinton 1951; Malicky 1969; Fukuda *et al.* 1978), then many species have secondarily lost their ant associations. Myrmecophily is nevertheless widespread within the family. Of the subfamilies described by Eliot (1973) (but including the Riodininae and Styginae; see Ehrlich 1958; Kristensen 1976; Vane Wright

1978), nothing is known of the early stages of the Styginae, and myrmecophily is not known from the Poritiinae; but ant associations have been recorded from the Lipteninae, Liphyrinae, Miletinae, Curetinae, Theclinae, Lycaeninae, Polyommatinae, and Riodininae (see Hinton 1951; Atsatt 1981b; Cottrell 1984; De Vries 1984; De Vries *et al.* 1986). In addition, Cottrell (1984) concludes that aphytophagy has arisen in at least eight independent lines of the Lycaenidae. Presumably, this has been due in part to the proximity of lycaenids to ants and sometimes to homopterans. Relationships that were initially mutualistic or parasitic (cf. Maschwitz *et al.* 1984) gave rise to predatory ones (Fukuda *et al.* 1978; Cottrell 1984).

Taken together, the integrated interaction among lycaenids, ants, and plants has meant that lycaenids have been exposed to wider possibilities for ecological segregation and diversification than those butterflies that rely simply on plants. They have had a bigger set of life-history permutations to draw upon. Circumstantial evidence for the role of ants in lycaenid diversification comes from the distribution of butterfly taxa and ant association. Holarctic lycaenids have a low frequency of ant association (see next section), and are relatively homogeneous in taxonomic terms: only 13 of the 33 lycaenid tribes recognized by Eliot (1973) are represented in the lycaenid faunas of the Nearctic and Palearctic. But lycaenids from other regions, which have a much higher frequency of ant association, are correspondingly more diverse: 32 of the 33 tribes are represented in the lycaenid faunas of the Ethiopian, Oriental, and Australasian regions, and 20 of these occur uniquely in those areas.

Ant associations may therefore explain in part why lycaenids are so diverse; they also suggest a mechanism that may have facilitated the process of this diversification. Lycaenids that require both host plants and attendant ants for survival will be able to live only in those areas where these resources coincide. The ranges of host plants and attendant ants are restricted, and thus the sites where their ranges actually overlap are even more limited and the distribution of the butterflies correspondingly more localized. This may account for the extremely patchy distribution of many species of ant-tended lycaenids (cf. Common and Waterhouse 1981). Restricted resources will restrict population sizes, and may result in geographic isolation of those populations. As it seems likely that the significant genetic changes associated with speciation are more likely to occur in small, isolated populations than in large, panmictic ones (Wright 1931, 1940; Lande 1976; Templeton 1980), it is possible that association with ants has been an important factor in generating the high species diversity that characterizes the Lycaenidae. Note that this argument is a relative one: that is, relative to other butterfly families, the Lycaenidae contain many more species, and relative to other butterflies, populations of myrmecophilous lycaenids may have experienced greater population subdivision and restriction.

Ants may have had yet another effect on population structure in the Lycaenidae. As described before, ant-associated lycaenids tend to lay their eggs in clusters, and the larvae and pupae often aggregate. Conspicuous aggregations of larvae and pupae make the location of potential mates easier and more predictable. Males of a species such as *Jalmenus evagoras* regularly patrol trees containing conspecific juveniles, and a great many males can compete for access to a single, teneral female. Females of *J. evagoras* mate only once, and virtually every female in a population is mated upon eclosion. However, males of *J. evagoras* vary greatly in their mating success: in a marked population, 57 per cent of males ($n = 35$) failed to mate at all, whereas one male mated seven times (Elgar and Pierce 1987). Thus, the aggregation of individuals into dense, localized areas and the conspicuousness of pupation sites promote intense competition among males for females. This would not occur in a butterfly species where individuals are widely dispersed and pupae are concealed and difficult to find. The importance of this behaviour for the present discussion is that if a small number of males are able to monopolize mating in a population, the effective population size will be reduced.

The biogeography of ant-associated species: an unresolved problem

A number of authors have suggested that mutualism should be more common in the tropics than in temperate zones (see discussion in May 1982; cf. Bristow 1984). For example, Howe (1975, p. 274) specifically suggested that associations between lycaenids and ants may be more common in the tropics. Similarly, Wood (1982, 1983) reviewed the life histories of 126 species of membracids, and noted that temperate regions appear to favour a solitary life habit, host specialization, and low reliance on ant mutualisms.

However, a comparison of the degree of ant association among herbivorous lycaenids in two geographic regions shows no pattern of ant association along a temperate-tropical gradient (Table 1). For the two regions in which comprehensive records of the lycaenid fauna are available and latitudinal comparison are possible (Common and Waterhouse 1981 for Australia and Fukuda *et al.* 1984 for Japan), latitude has no effect on the frequency of lycaenid–ant associations; the larvae of species in tropical and subtropical regions are as likely to be tended by ants as the larvae of species in temperate regions. (In the Japanese fauna, the subtropical species are those recorded from the island of Okinawa, and it is therefore possible that island biogeographic effects could obscure latitudinal patterns; these data are presented only tentatively to support the more robust Australian pattern.)

To estimate the prevalence of ant association in different biogeographic regions, I have collected data from sources where attempts have been made to catalogue the entire lycaenid fauna of a particular region without bias to ant-associated life-history characteristics. The references by region are as follows: Common and Waterhouse 1981 for Australia; Fukuda *et al.* 1984 for Japan;

Bell 1915–20 for India; Howe 1975, Downey and Allyn 1979, Dornfeld 1980, Emmel and Emmel 1973, Ferris and Brown 1981, Scott 1986, and J. C. Downey (pers. com.) for North America; Forster and Wohlfahrt 1955, Malicky 1969, Kitching and Luke 1985, and Higgins and Riley 1970 for Britain and Europe; Clark and Dickson 1971, Claassens and Dickson 1980, Henning 1983a, Farquharson 1921, and Lamborn 1913 for South Africa. The data are broken down by species and genera. A species was scored as 'obligately' associated with ants if it was recorded as always tended by ants during at least some portion of its lifetime, and 'facultatively' associated if it was noted as sometimes tended by ants. Using this definition, parasitic species whose larvae feed on ant brood during all or a portion of their lifetimes are also all 'obligately' associated, but I have placed them in a separate category, since the nature of their relationship with ants is so distinct. A genus was considered to be ant-associated if 50 per cent or more of its species associate with ants, and obligately, facultatively, or parasitically associated if 50 per cent or more of its species fall into one of these categories.

The intriguing pattern that emerges from this study of ant attendance and biogeography in the Lycaenidae is that association in general, and obligate interactions in particular, are far less common among Holarctic species than among those with Oriental, Ethiopian, and Australasian distributions (Table 2; Fig. 1). This pattern is suggestive of a Gondwanaland–Laurasia split in ant-associated and non-ant-associated lineages in the Lycaenidae. If the pattern is to be explained in terms of such a faunal split, then two evolutionary conditions must be fulfilled:

(1) the distribution of lycaenid groups should correspond to their phylogeny (i.e. the lycaenid fauna of one region should be uniquely derived from a lineage or lineages which are not represented in the faunas of other regions);

(2) the distribution of ant association within the Lycaenidae should also correspond to the group's phylogeny (i.e. given that all lycaenids are thought to be ancestrally myrmecophilous and that many extant species are not ant-associated, then entire lineages should be characterized by the derived state of non-myrmecophily).

By using the distribution and phylogenetic data presented by Eliot (1973) in his higher classification of the Lycaenidae (pp. 457 and 471, respectively), it is possible to examine these conditions and thereby assess the specific scenario that, subsequent to the Laurasia–Gondwanaland biogeographic split, the Holarctic lycaenids were derived from a lineage or lineages of lycaenids that did not associate with ants, whereas the remaining fauna was derived from a lineage or lineages that did associate with ants. Quite simply, the answer to this is no—such a scenario is not possible.

(1) There is no Holarctic–non-Holarctic dichotomy in Eliot's phylogeny. The bulk of Holarctic genera are in the subfamilies Theclinae and Polyommatinae, and these are both heavily represented in other regions as well. This taxonomic overlap is also seen at lower taxonomic ranks: Eliot's distributional data for tribes shows no evidence of a faunal split. Only one (the Tomarini) of the thirty-three tribes of the Lycaenidae recognized by Eliot is unique to the Holarctic. Furthermore, this is a small group, and in terms of overall numbers of species and/or genera, is of little importance. The only region where lycaenid phylogeny appears to be related to the historical effects of continental drift is the Neotropics, where a separate lineage, the Riodininae, has proliferated. Unfortunately, little is yet known about the life histories of the lycaenid and riodinid fauna of this region as a whole (although ant associations seem to be common; see Robbins and Aiello 1982; Callaghan 1977, 1979, 1981–2; Ross 1966; Schremmer 1978; Horvitz and Schemske 1984; P. J. De Vries, pers. com.).

Table 2

The proportion of ant-associated lycaenid butterflies from different geographic and biogeographic regions. Refer to text for sources of data and definitions of 'obligate', 'facultative', and 'parasitic' associations

		Associated with ants (%)				Not associated with ants (%)
Region	N	Obligate	Facultative	Parasitic	Total	
Laurasia						
Palearctic						
Europe (spp.)	102	1	25	4	30	70
(gen.)	43	2	28	2	32	68
Japan (spp.)	72	1	28	6	35	65
(gen.)	51	2	31	6	39	61
Nearctic						
North America (spp.)	126	1	17	0	18	82
(gen.)	39	0	23	0	23	77
Gondwanaland						
Australasian						
Australia (spp.)	102	31	37	4	72	28
(gen.)	37	16	49	5	70	30
Ethiopian						
South Africa (spp.)	126	10	66	17	93	7
(gen.)	38	5	79	5	89	11
Oriental						
India (spp.)	60	22	53	0	75	25
(gen.)	36	25	53	0	78	22

(2) The distribution of ant association within the Lycaenidae is independent of phylogeny. For example, as mentioned before, most of the subfamilies of the Lycaenidae contain both ant-associated and non-ant-associated tribes; individual tribes often contain both ant-associated and non-ant-associated genera; and many genera contain both ant-associated and non-ant-associated species. From this, it would appear that the loss of myrmecophily

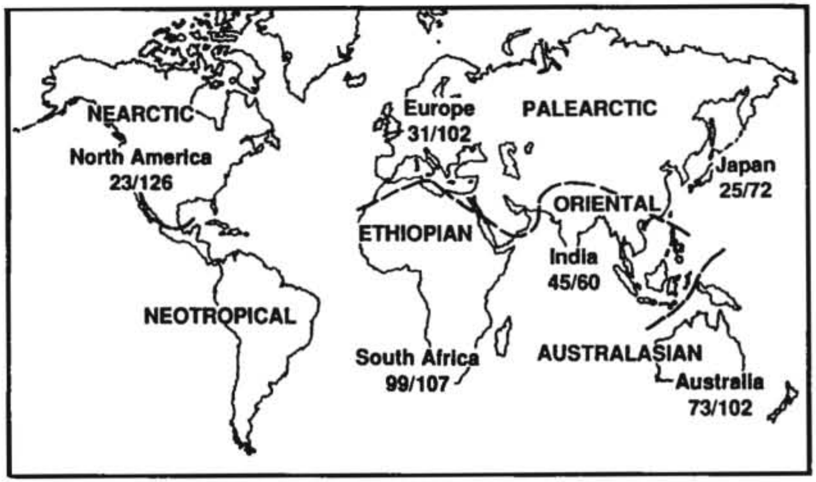

Fig. 1. The biogeographic distribution of species in the butterfly family Lycaenidae whose larvae associate with ants. For each region, the number of lycaenid species recorded to associate with ants out of the total number of lycaenid species from that region whose life histories have been described is indicated. Refer to text for sources of data and Table 1 for a breakdown of the kinds of associations found within each region.

in the Lycaenidae has occurred relatively recently in evolutionary terms, and relatively haphazardly with respect to phylogeny.

Assuming the validity of Eliot's phylogeny, there is no doubt from the analysis above that the observed pattern of ant association cannot be explained by the distribution of the lycaenids themselves. Nevertheless, the apparent correlation between ant association and Gondwanaland-derived geographic regions may still be explicable in terms of historical biogeography. The ecological conditions necessary for the maintenance of ant associations in the Lycaenidae include every level of interaction: ants, plants, lycaenids, parasitoids, and predators. Have the distributions of ants, plants, and natural enemies with which the lycaenids are associated been determined by the Laurasia–Gondwanaland split? If so, is it their distribution which drives the pattern of ant association seen in Fig. 1? An adequate analysis of these questions is beyond the scope of this paper, but a few examples immediately come to mind. Among the possible food plants of lycaenid butterflies, both *Acacia* (Maslin and Hopper 1982) and mistletoes in the Loranthaceae (Barlow 1981) are thought to have radiated in Gondwanaland regions, and as mentioned before (see also Pierce 1985), these plants may be particularly suitable food for lycaenids with ant associations. Gondwanaland-derived regions may also contain a greater diversity and/or abundance of hostile ants such as the predaceous genus *Myrmecia*, and these could act as a potent selective force in maintaining a high degree of ant attendance in these regions (Commonwealth

Scientific and Industrial Research Organization 1970; also see references in Gauld 1986).

However there does not appear to be a readily discernible historical basis to the distribution of ant taxa that associate with lycaenid butterflies. These commonly include species in the genera *Iridomyrmex*, *Oecophylla*, *Camponotus*, and *Crematogaster*, and the most striking feature that these genera share is that they are often the ecologically dominant ants in the regions where they occur (W. R. Brown, pers. com.). The first three of these genera are known from early Tertiary fossils, while *Crematogaster* appears to be a more recent genus, whose first appearance is in the Dominican amber of the late Miocene (Wilson 1971). Although fossils of *Iridomyrmex* occur world-wide, the extant members of the genus are distributed mainly in the Southern Hemisphere (Brown 1973; Greenslade 1979; Greenslade and Halliday 1982; Morton 1982). Likewise, although it appears to have been Laurasian in its origin, *Oecophylla* now consists of only two species, with an African and an Indo-Australian distribution respectively. Both fossil and extant species of *Camponotus* and *Crematogaster* have world-wide distributions, although *Crematogaster* is now more predominant in the Northern Hemisphere (Brown 1973). Given the fossil record of potential ant associates and the extant pattern of such associations, it seems that opportunism and 'colonization' of dominant attendant ant species that have wide distributions and large colony sizes have been the most important variables in determining the choice of the majority of lycaenid ant partners.

At least one other class of explanation exists for the pattern shown in Table 2: simple faunal convergence between the regions in question. Similarities in climate, soil, and other biotic and abiotic features in South Africa, India, and Australia may have promoted convergence in lycaenid–ant associations in these areas. This argument has already been used to explain the high incidence of ant-dispersed plants in both South Africa and Australia (Milewski and Bond 1982; Westoby *et al.* 1982). Indeed, while convergence in characteristics such as climate and soil composition may have contributed significantly to the similarly high incidences of myrmecochorous plants in these regions, it would be interesting in light of the pattern shown in Table 2 to examine the comparative phylogeny and biogeography of myrmecochorous plants.

In conclusion, the biogeographic distribution of ant-tended and non-ant-tended species in the Lycaenidae provides a striking pattern that begs explanation. It gives the initial appearance of having been shaped by the historical events of continental drift, and, were this the case, it would be an interesting example of how major geological events have influenced not only the distribution of a single taxonomic group, but also the distribution of multi-species interactions. However, the explanation of the pattern is by no means straightforward. A consideration of the phylogeny of the Lycaenidae rules out the possibility that the pattern has been generated by the distribution of the Lycaenidae alone. However, the existence of suitable host plants and/or lycaenid enemies are equally important in this evaluation, and it would be interesting to examine their relative distributions, abundances, and phylogenies. Convergence between faunas in different geographic regions is a plausible alternative explanation. More information about the entire lycaenid fauna from the Neotropics, and a detailed cladistic analysis of the Lycaenidae that builds upon the foundations laid by Eliot will be necessary before any conclusions can be drawn.

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