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The Effects of Ant Mutualism on the Foraging and Diet of Lycaenid Caterpillars

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Introduction

Larvae of species in at least 10 families of the Lepidoptera associate with ants (Hinton 1951; Maschwitz et al. 1986), and of these the great majority are members of the Lycaenidae. About half of the Lycaenidae whose life histories have been described are myrmecophilous (Pierce 1987 cites records for 433 species from 6 biogeographic regions) and, with more information, this proportion is likely to be even greater (e.g., Fiedler 1991 provides thorough data for 118 species from Europe and North Africa alone). Ant association is also commonly found among species of the closely related taxon, the riodinids, although the frequency may not be as great as in the Lycaenidae (DeVries 1990b). Since together, these groups comprise about 30% of the some 17,280 species of butterflies estimated to occur worldwide (Shields 1989), larval association with ants is clearly a significant component of butterfly ecology.

Lycaenid–ant associations can be parasitic, commensal, or mutualistic (Hinton 1951; Atsatt 1981b; Cottrell 1984; Pierce 1987). Mutualisms in which the fitness of each partner is increased by the action of the other appear to be by far the most common type of interaction: the larvae of many species have specialized glands that visibly secrete droplets of food that are consumed by ants. Not only do attendant ants not attack the larvae themselves, but they often appear to protect them against other, potential enemies. Although some degree of chemical deception of ants by lycaenids is possible, it seems likely that ants in the majority of these relationships are harvesting substantial food rewards and are not being fooled by the caterpillars. To date, quantitative evidence assessing the costs and benefits for each partner in these associations is available for only a few lycaenid–ant and riodinid–ant systems (Ross 1966; Pierce and Mead 1981; Horvitz and Schemske 1984; Pierce and Easteal 1986; Pierce et al. 1987; DeVries 1988, 1990a, b; Fiedler and Maschwitz 1988, 1989a, b; Nash 1990; Savignano 1990; Baylis and Pierce 1991b). Our discussion here concentrates mainly on these mutualistic associations.

This chapter will examine the nature of the nutritional hurdles imposed by lycaenid–ant mutualisms and the responses of lycaenids to those challenges. We will begin with a brief overview of some of the effects that ants may have had on the dietary choices of lycaenid butterflies. We will then focus our discussion on *Jalmenus evagoras*, the species that has been the subject of our research in this area, and evaluate some of the physiological constraints imposed by the need to secrete rewards for ants as well as evidence for physiological and behavioral responses to these constraints.

Ants involved in lycaenid–ant interactions typically obtain their food from a variety of sources, and no relationships have been described in which attendant ants rely entirely on the secretions of lycaenid larvae for sustenance. However, lycaenids vary considerably in the strength of their associations with attendant ants. In some species, larvae appear to appease ants but have no other direct interactions with them; in others, perhaps the majority, larvae not only appease ants, but are intermittently tended by any of a large number of different species; and in still others, larvae are continuously tended by a single species of ant. This variation makes it difficult to generalize about the effects of ants on lycaenid foraging. Moreover, despite a valuable higher classification of the family which helps to distinguish many of the main taxa (Eliot 1973), the absence of a cladistic phylogenetic analysis restricts our ability to perform informative comparative studies across species.

There are, nevertheless, a number of common themes in lycaenid–ant interactions. Myrmecophilous lycaenid larvae have remarkably thick cuticles that are contoured in ways that protect the vital organs against occasional bites by attendant ants (Malicky 1970). The pupae and sometimes the larvae of many species stridulate, and these vibrations may serve as important communication signals for their attendant ants (Downey 1966; Downey and Allyn 1978; DeVries 1990a).

The association is primarily mediated through several specialized exocrine glands that secrete substances that appease ants, and in many species, reward them. The composition of these secretions has been partially analyzed for only a few species, and none has been fully characterized for all possible chemical components (Henning 1983b). This is particularly true for the pair of lateral tentacular organs found on the eighth abdominal segment of many species which secrete volatile chemicals that appear to mimic ant alarm signals (Claassens and Dickson 1977; Fiedler and Maschwitz 1987). Yamaguchi (1988) mentions that dendrolasin may be involved in interactions between the Japanese species, *Shirozua jonasi* and its attendant ants, and points out that dendrolasin can also function as a warning pheromone for ants such as *Lasius fulginosis*.

Secretions from the "dorsal organ" found on the seventh abdominal segment of many species were examined from larvae of *Polyommatus (Lysandra) hispana*, and found to contain largely carbohydrates, including fructose, glucose, sucrose, and trehalose in total concentrations ranging from about 13 to 19% by weight, and only trace amounts of the amino acid methionine (Maschwitz et al. 1975). Secretions from the dorsal organ of the Australian lycaenid, *Jalmenus evagoras*, contained sucrose, fructose, and glucose in concentrations of about 10%, as well as the amino acid serine, in concentrations that varied diurnally from about 20 to 40 mM (Pierce 1989). Amino acids were also detected in secretions from the many single-celled glands scattered in the epidermis of the larvae, called "pore cupolae" organs (Malicky 1969), and similar structures in the pupae (Kitching 1983), although these glands are likely to secrete additional compounds (Henning 1983b). The dorsal organ secretions of two congenors of *J. evagoras* produced similar amounts of amino acids, whereas those of a third produced aqueous solutions of a small, unidentified polypeptide (Pierce 1989). Among the Riodinidae, glands analogous to the dorsal organ, the "tentacle nectary organs" of *Thisbe irenea* were found to contain 10% sugar solutions and relatively high concentrations of a number of amino acids (DeVries 1988; DeVries and Baker 1989).

Lycaenid secretions differ in at least one significant way from the honeydew of Homoptera, with which they are frequently compared. Homopteran honeydew is excreted as a byproduct of feeding on plant phloem and xylem (Way 1963). Homopterans are known to modify aspects of their honeydew in response to attendant ants, including the rate of production, and the manner in which the honeydew is presented (Mittler 1958; Banks and Nixon 1958; Auclair 1963; Dixon 1985; Letourneau and Choe 1987). However, since it is essentially an excrement, honeydew is likely to be inexpensive for the homopterans to produce, and they produce it whether ants are there to receive it or not.

In contrast, lycaenids must synthesize their secretions actively. Amino acid secretions are metabolically costly to produce since they require diverting valuable protein resources from growth and development to defense: not surprisingly, lycaenids typically present these secretions only on solicitation by attendant ants. Indeed, larvae of *J. evagoras* raised without ants pupate at a larger size than those raised with ants (Pierce et al. 1987). It is difficult to make meaningful comparisons between the composition of these lepidopteran secretions and that of homopteran honeydew since so few species have been analyzed. However, lycaenid and riodinid secretions appear to contain lower concentrations of carbohydrates than most honeydews, and in some cases, higher concentrations of amino acids (Auclair 1963; Dixon 1985).

Lycaenid larvae benefit from ant associations in at least two ways. First, by secreting chemicals that appease ants, they are protected against the ants themselves that might otherwise be threatening predators (Malicky 1970). Second, experiments with several species have shown that attendant ants protect lycaenid larvae from predators and parasitoids (e.g., Pierce and Easteal 1986; Pierce et al. 1987; DeVries 1991; Fiedler and Maschwitz 1988, 1989a, b; Savignano 1990). For example, the presence of attending ants was estimated to make a four to 12-fold difference in survival to pupation of larvae of the North American lycaenid, *Glaucopsyche lygdamus* (Pierce and Easteal 1986). The degree of protection afforded by attendant ants depends on characteristics such as the species of attendant ants, the density of predators and parasitoids in the habitat, and the phenologies of the different interacting parties (e.g., Pierce and Mead 1981; Bristow 1984).

Ant-associated lycaenid larvae thus live with unusual dietary constraints: not only must they consume sufficient food for their own development, but they must additionally supply food to their ant guard. These nutritional constraints depend in part on the nature of the rewards provided to the ants, and these in turn depend on the dietary preferences and alternative food sources available to the ants. For example, a lycaenid larva competing with homopterans and other nectar-secreting sources for the attention of ant mutualists may be under considerable pressure to produce rewards that are more attractive to attendant ants than the carbohydrates found in most honeydews. This may explain why the secretions of *J. evagoras* contain concentrated free amino acids as well as simple sugars. These amino acids can be shown to act as powerful phagostimulants for the attendant ant species, and may ensure that the larvae are continuously tended by ants, even when other honeydew-secreting insects are present (Pierce 1989).

Although amino acid secretions may be expensive to produce, populations of *J. evagoras* whose ants are experimentally excluded are preyed on so heavily that they cannot survive, meaning that the attraction and provision of an ant guard is, for this species, mandatory (Pierce et al. 1987). So, while Lawton's and McNeill (1979) herbivorous insect was caught between the devil of plant defenses and the deep blue sea of malnutrition, a myrmecophilous lycaenid caterpillar must contend not only with the same devil, but with a sea that is even deeper and bluer because of the additional nutritional demands imposed by its ant guard.

The Effect of Ant Protection on Lycaenid Diets

Protection by ants may have direct effects on the spatial and temporal foraging patterns of lycaenid larvae. Myrmecophilous lycaenid larvae occupy what has been called "enemy-free space" (Lawton 1978; Atsatt 1981b; Jeffries and Lawton 1984), areas in which the threat of predation and parasitism has been reduced because of the activities of attendant ants. Thus larvae may be able to feed in places, or at times of day, which would not be possible without ant protection. Feeding on the terminal foliage where leaves are more nutritious, and feeding during the day despite increased visibility to predators can be of considerable advantage to lycaenid larvae: the consumption of more nutritious food, and consumption throughout the day, permit shorter development times (Slansky and Scriber 1985). A good example of this is provided by *J. evagoras*. Larvae of *J.*

evagoras feed on acacia trees and are tended by ants in the genus *Iridomyrmex*. The larvae aggregate, and feed both during the day and night, often forming clearly visible congregations.

However, such apparency is rather exceptional among lycaenids. On the opposite extreme, protection by ants may also encourage behavioral crypsis among lycaenids such as the Australian species *Ogyris genoveva:* larvae of this butterfly shelter during the day in "byres" or earthen "corrals" constructed at the base of trees by their attendant ants, species of *Camponotus*, and emerge only at night to feed on the foliage of mistletoe hanging in the host trees (Common and Waterhouse 1981). Similarly, the ant-tended larvae of the Adonis Blue, *Polyommatus (Lysandra) bellargus*, have crepuscular activity patterns (Thomas 1983).

The foraging patterns adopted by different species of ant-associated lycaenids must depend in part on the activity patterns and the quality of protection offered by their ant associates. Lycaenids whose attendant ants are assiduous tenders, diurnally active, and possess relatively large colony sizes and/or well-developed systems of mass recruitment may be able to feed more openly. In contrast, those whose attendant ants are relatively weak tenders, nocturnal or crepuscular foragers, and possess small colony sizes and/or poor means of mass recruitment might resort to a more cryptic mode of foraging.

Foraging lycaenids may be influenced not only by the temporal activities of their attendant ants, but also by their spatial distributions. Lycaenids that associate with ants are more likely to lay their eggs in clusters than their untended counterparts, and the larvae and pupae are also more likely to aggregate (Kitching 1981). Feeding in aggregations may bring benefits in terms of attracting a larger, more efficient ant guard and facilitating foraging and handling time, especially for young larvae (Pierce et al. 1987). However, it can also incur costs: larvae of *J. evagoras* frequently consume all the available foliage on their host plants. Larvae must either find a new host plant or starve, although in some cases, feeding on extrafloral nectar or honeydew from homopterans may allow larvae on defoliated host plants to persist for prolonged periods.

Since selection favors myrmecophilous lycaenids that feed in places where the presence of associated ants reduces the density of potential enemies, attendant ants may also affect lycaenid host plant choice (Atsatt 1981b). Thus lycaenids may be more likely to feed on plants with extrafloral nectaries or a homopteran fauna, both of which serve to attract ants to the plant. Larvae of the Lipteninae, a subfamily of the Lycaenidae, are associated with ant columns on tree trunks, and feed on lichens, fungi, and algae found under the bark of trees. Characteristics of the host plants themselves, such as their growth form and/or relative degree of "apparency," may further influence the ant environment and thereby the lycaenid fauna (Malicky 1969; Atsatt 1981b).

Proximity to ants that farm a variety of nectar-producing sources has presumably led to the behavior seen among many lycaenid and riodinid larvae of imbibing nectar themselves, including extrafloral nectar and homopteran honeydew (Cottrell 1984). This nectar feeding is a curious sight, and has led to the belief that these caterpillars are parasitizing ant–plant and ant–homopteran interactions, possibly as a means of reducing the cost of producing ant attractants themselves (Horvitz and Schemske 1984; Maschwitz et al. 1984; Horvitz et al. 1987; DeVries and Baker 1989). For example, larvae of *Lachnocnema bibulus* feed on the honeydew of jassids, membracids, and psyllids, and larvae of *Shirozua jonasi* drink the honeydew of coccids and aphids (Hinton 1951). The larvae of *J. evagoras* and some of its congenors frequently drink extrafloral nectar from the host plant as well as homopteran honeydew, although this behavior is more often observed when ants are in attendance and disappears almost entirely when ants have been experimentally excluded (Pierce and Elgar 1985; unpublished observations). Larvae of the Japanese species, *Niphanda fusca*, feed primarily on regurgitations from their host ants (Fukuda et al. 1984). Moreover, the carnivorous consumption of homopterans themselves is widespread in the Lycaenidae: Cottrell (1984) cites examples in eleven genera from four subfamilies.

A number of lycaenid species live in, or directly around, ant nests or shelters. Some of these species maintain herbivorous diets: larvae of *Hypochrysops apollo*, which live in ant nests made in the ant plant *Myrmecodia beccarii*, feed on internal plant tissues (Common and Waterhouse 1981), and *Anthene emolus* lives in nests woven from the leaves of the tree *Saraca thaipingensis* by the weaver ant *Oecophylla smaragdina*, and feeds on the leaves of the tree (Fiedler and Maschwitz 1989b). This trend has been extended beyond mutualism to myrmecophagy by the parasitic species *Liphyra brassolis*, whose larvae prey on the ant brood within the nests of the weaver ants (Dodd 1902). These larvae possess an impressive array of adaptations for preying on ants, including an exceptionally thick and sclerotized cuticle, a fringe of hairs along the ventral side that appear to aid the larvae in clamping down on the substrate and resisting attempts by ants to expose the vulnerable ventral surface, as well as larvae antennae-like structures that are used in finding ant brood. The majority of other lycaenid species that parasitize ants do so by chemically mimicking aspects of their recognition signals, thereby fooling the ants into accepting them into the brood chamber of the nest where they then set about devouring the brood (Cottrell 1984; Thomas et al. 1989; Fiedler 1990b).

The necessity for myrmecophilous lycaenids to be found in, or near to ant nests or foraging places may act to limit the diversity of possible diets available to such lycaenids. However, myrmecophily may have also promoted diversification of lycaenid diets, not only to nectar feeding and to the carnivorous extremes exhibited by homopterophagous and myrmecophagous species, but also to a wider range of host plants among the strictly herbivorous taxa. Ant-dependent oviposition appears to be relatively common among the strongly myrmecophilous species. Caged females of *Ogyris amaryllis* laid larger egg batches on branches where they encountered ants than on those where ants had been excluded (Atsatt 1981a). When presented with trees bearing attendant ants and larvae, and trees with just larvae, females from one population of *J. evagoras* laid 86% of their eggs on the trees with ants and larvae (Pierce and Elgar 1985). Indeed, females could be induced to lay eggs on wooden dowling in the field, provided that pupae of *J. evagoras* and attendant ants were present on these artificial substrates (Atsatt, Pierce, and Smiley unpublished data). Pierce and Elgar (1985) cite 46 species of lycaenids, from 29 genera in 5 subfamilies, in which ant-dependent oviposition has been suspected or described.

Oviposition "mistakes" induced when appropriate attendant ants occur on plants other than the customary host species might therefore be especially common among ant tended lycaenids. For example, the larvae of *Hypochrysops ignitus* feed on at least 12 different plant families, but they are tended only by the ant *Iridomyrmex nitidus* (Common and Waterhouse 1981). Depending on the relative costs and benefits and the different species involved, lycaenids that have a mobile ant defense may also be able to shift hosts more readily than species that rely on sequestering chemical defenses from their food plants. Pierce and Elgar (1985) compared the diet breadth of 282 species of ant-associated and non-ant-associated lycaenids and found that, in general, lycaenids that are tended by ants feed on a greater number of host plant families and genera than their non-ant-attended counterparts. Myrmecophily may not be the only reason for increased diet breadth (Fiedler 1990a); however, the existence of ant-dependent oviposition provides a plausible mechanism promoting host expansion in myrmecophilous taxa.

It is tempting to speculate from these observations that ant association may have a paradoxical effect on the host plant range of lycaenids: ant dependence might simultaneously restrict the number of adequate feeding niches and facilitate host range expansion. Ant-induced host plant sampling may also help to explain the wide taxonomic diversity of food sources utilized by the Lycaenidae compared with other families of butterflies (Ehrlich and Raven 1965). The diets of herbivorous lycaenids include fungi, blue-green algae, lichens, ferns, cycads, conifers, bamboos, mistletoes, oaks, and legumes (Atsatt 1981b; Henning 1983a; Pierce 1987).

Because they decide where to lay eggs, female butterflies by and large determine the ant environment of the larvae. However, the juveniles of *J. evagoras* aggregate, and ovipositing females are attracted to their own juveniles as well as to ants (Pierce and Elgar 1985). Thus responses by the larvae to the presence or absence of ants can influence both the immediate ant environment, and the ant environment of the next larval generation. For example, larvae on plants where ant densities are high pupate in higher locations than larvae on plants where ant densities are low (Carper 1989). Presumably both the presence of larvae (indicating successful survival), and the relative degree of visibility of their pupation sites provide valuable feedback to females about the ant environment of potential host plants.

Presumably this is one of the mechanisms by which species specificity has arisen in certain mutualistic lycaenid–ant interactions. If females oviposit in response to the presence of conspecifics, then any ant that is a good enough tender that the larvae survive will enjoy an enhanced level of oviposition on trees where it is tending. If a particular ant species is an unusually proficient tender, then over time, the ant species itself, even in the absence of conspecific juveniles, might be sufficient to elicit enhanced levels of oviposition on appropriate host plant species. As long as female lycaenids lay at least some of their eggs on host plants, either not occupied by ants and/or visited by other species of ants, then this mechanism would allow them to sample the available ant fauna on a continuous basis. Should the ant fauna change for any reason (i.e., the "customary" ant associate become scarce, and/or a new species arise that is a better tender than the original associate), selection would cause the butterflies to change their affiliation accordingly.

Constraints Imposed by Secretion

Nitrogen and water are particularly important currencies in the nutrition of herbivores (McNeill and Southwood 1978; Strong et al. 1984). The growth rates and feeding efficiencies of herbivorous insects are strongly correlated with the relative ratio of nitrogen and water in their diet (Scriber 1977; Scriber and Slansky 1981; Slansky and Scriber 1985). Phytophagous ant-associated lycaenid larvae face these dietary constraints as well as having to secrete to ants aqueous solutions of carbohydrates and proteins. The amount secreted can be considerable. Sixty-two larvae of *J. evagoras* on a single tree were found to provide for ants approximately 400 mg dry biomass over a 24-hour period (Pierce et al. 1987). A larva of the European lycaenid, *Polyommatus (Lysandra) coridon* was estimated to produce 22–44 μl of solution in its lifetime, containing approximately 3.5–7.0 mg of dry biomass (Fiedler and Maschwitz 1988). The total volume produced by a single final instar of *Anthene emolus* is at least 80 μl, which, assuming a carbohydrate concentration of 15% (Maschwitz et al. 1975), contains approximately 12.7 mg of carbohydrate (Fiedler and Maschwitz 1989b).

Variation in the quality of lycaenid secretions is doubtlessly generated by a complex set of interacting variables, including the strength of predation and/or parasitism in a habitat, the degree of dependence of the lycaenid larvae on attendant ants for defense, the nature of the host plant, the dietary requirements of the ants, and the presence of alternative food resources for the ants. Selection should favor individual lycaenids that receive the maximum benefit of ant defense in exchange for the minimum cost of ant attraction. Thus we might expect to find considerable flexibility and variability in the nature of the secretions of different species and even of separate populations of the same species found in different habitats.

The costs of secretion can have far-reaching consequences. To investigate some of these consequences, we examined whether larvae of *J. evagoras* could

Table 12.1. Summary of the Effect of Ants on the Nutrition and Growth of Fifth Instar Larvae of J. evagoras[a]

	With ants[b]	Without ants[b]
Size at start of final instar	<	>
Development time	=	=
Relative consumption rate	=	=
AD	=	=
Relative growth rate	<	>
Size at start of pupal instar	<<	>>

[a] AD, approximate digestibility, a measure of the proportion of ingested food that is digested. From Baylis (1989) and Baylis and Pierce (1991a).

[b] <, significantly smaller; >, significantly greater; =, no significant difference.

compensate physiologically for the dietary cost of maintaining an ant guard. In other insects, compensation for changes in diet quality can occur by consuming more food, consuming food of a higher nutritional quality, altering digestive efficiencies (reviewed by Simpson and Simpson 1989; also see Fiedler 1990a), and/or extending development time (Mattson 1980).

We reared *J. evagoras* larvae from eggs under uniform conditions and fed them on cuttings from potted *Acacia* plants (Baylis 1989; Baylis and Pierce 1992). Half of the larvae were reared with attendant ants from a laboratory colony of *Iridomyrmex (anceps* species group); the other half were untended. The development time, relative consumption rate and approximate digestibility (AD; a measure of the proportion of ingested food that is digested) of final instar larvae were measured using the gravimetric method of Waldbauer (1968). The presence or absence of ants did not have a significant effect on any of the three compensatory methods examined (Table 12.1). As a consequence, final instar larvae reared with ants had a significantly lower growth rate than larvae reared alone (Baylis 1989; Baylis and Pierce 1992). This result agrees with the previous finding that larvae of *J. evagoras* reared in the laboratory on trees from which ants have been excluded are larger than those reared on trees with ants (Pierce et al. 1987).

It thus appears that larvae of *J. evagoras* do not compensate for the nutrient loss to ants; they simply bear the loss by growing less. Reduced growth represents a real cost to *J. evagoras:* both the lifetime mating success of males and the fecundity of females are positively correlated with relative adult size (Elgar and Pierce 1988).

The inability of larvae of *J. evagoras* to compensate for the nutrient loss to ants suggests that the nutrients, particularly nitrogen and water, may be especially limiting in the survival and growth of the larvae. There is good evidence that this is the case. In a further experiment, young, potted seedlings of *Acacia decurrens* were either given water containing a nitrogenous fertilizer, or water alone. The foliage of plants treated with fertilizer had a higher nitrogen content than the unfertilized plants, although this covaried with a number of other nutrients found in the plants (Baylis and Pierce 1991a). Under field conditions, final instar larvae of *J. evagoras* feeding on the plants treated with fertilizer attracted a larger ant guard than those feeding on unfertilized plants (Fig. 12.1). In the absence of caterpillars, ants showed no preference for either plant type.

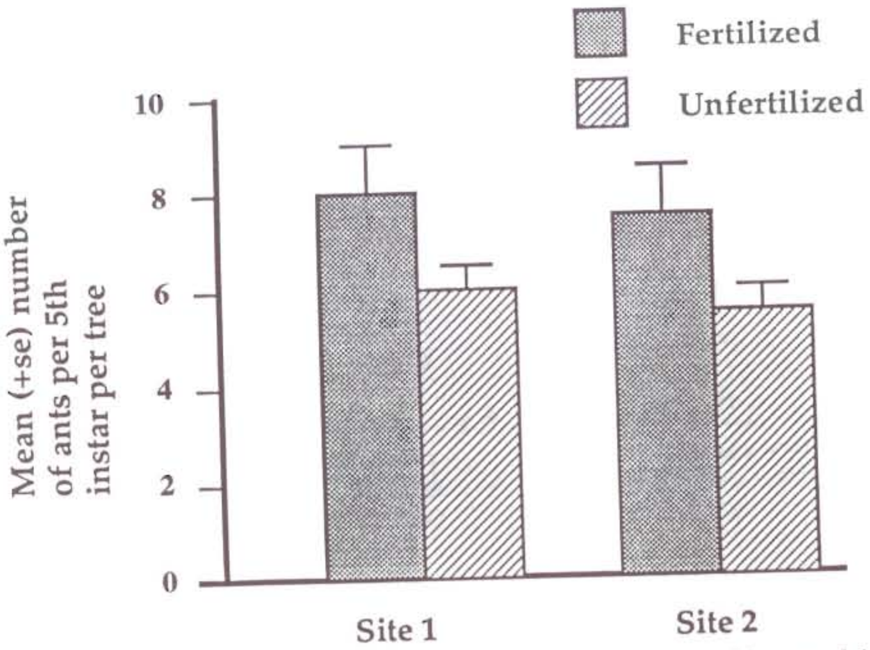

Figure 12.1. The Effect of Host Plant Quality on Ant Attendance of Larvae of *J. evagoras*. Mean number of ants (± SE) tending fifth instar larvae feeding on potted host plants that had been treated with nitrogenous fertilizer (solid columns) or not treated with fertilizer (hatched columns). Measurements were taken for ants tending larvae at two field sites in Mount Nebo, Queensland, Australia.

These results indicate that the ant attractants secreted by larvae of *J. evagoras* vary as a function of diet quality. Not only did caterpillars on plants treated with fertilizer attract a larger ant guard, but they also survived better in the field over a 10-day period than did larvae on unfertilized plants (Fig. 12.2). Control larvae reared in a screened bush house from which tending ants and predators were excluded survived equally on both types of plant. We therefore attribute the increase in survival rate to the attraction of a larger ant guard (Baylis and Pierce 1991a).

Thus host plant quality indirectly influences the survivorship of larvae of *J. evagoras* through altering the level of ant defense. As with other phytophagous insects, host plant quality also directly affects larval growth (Baylis 1989). Pupae of *J. evagoras* were collected from 82 trees of *Acacia melanoxylon* at Ebor in

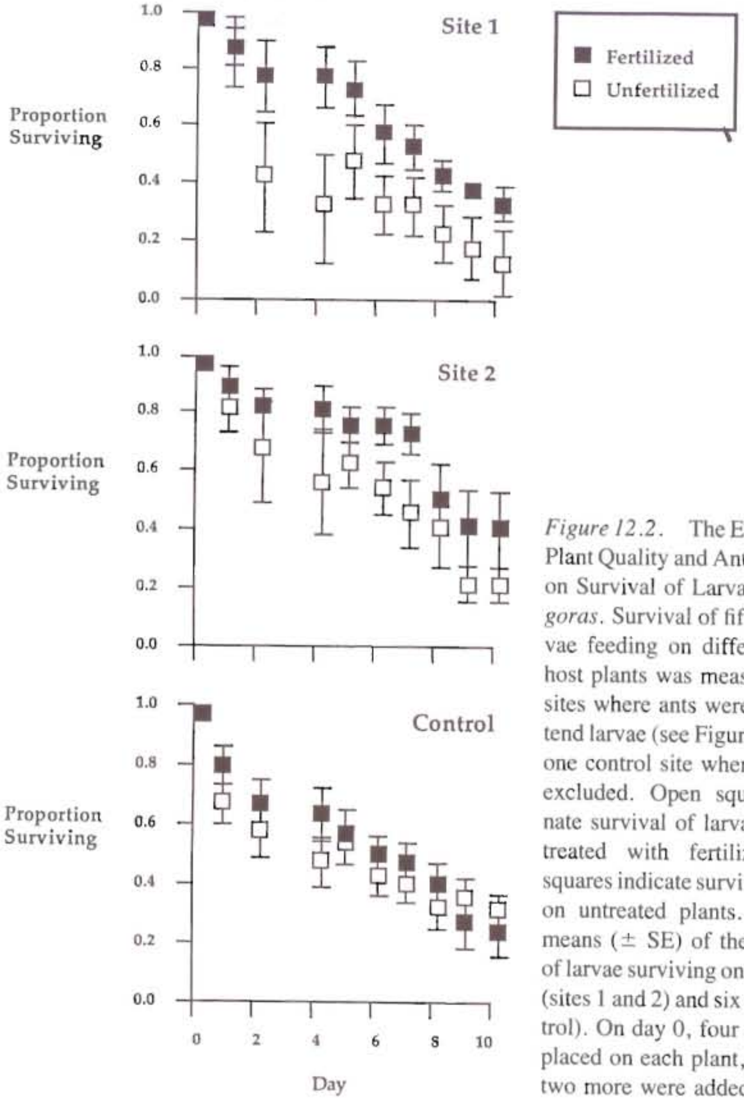

Figure 12.2. The Effect of Host Plant Quality and Ant Attendance on Survival of Larvae of *J. evagoras*. Survival of fifth instar larvae feeding on different quality host plants was measured at two sites where ants were allowed to tend larvae (see Figure 12.1), and one control site where ants were excluded. Open squares designate survival of larvae on plants treated with fertilizer; closed squares indicate survival of larvae on untreated plants. Points are means (± SE) of the proportion of larvae surviving on three plants (sites 1 and 2) and six plants (control). On day 0, four larvae were placed on each plant, and day 4, two more were added.

New South Wales, Australia. Although all the trees were of the same species, they were of two types: 58% of the trees had both young and mature leaves (YM), while the remaining 42% of the trees had only mature leaves (M). We found that both the young and mature leaves of the YM trees had higher nitrogen and water contents than the mature leaves of the M trees (Table 12.2). This suggests that the larvae that fed on the YM trees had a diet of higher nutritional quality than those that fed on M trees. Not surprisingly, the adults reared from the pupae collected from YM trees were larger than those reared from pupae collected from M trees.

Table 12.2. The relationship between Percent Nitrogen and Percent Water Content of Young and Mature Leaves, and the Weights of Adults of J. evagoras. *Data are shown for YM trees (those with both young and mature leaves) and M trees (those with just mature leaves)*[a]

	YM trees			M trees			Unpaired
	Mean	SD	*n*	Mean	SD	*n*	*t* value
Nitrogen (dry weight) (%)							
Y	3.02a	0.56	48				
M	2.70a	0.32	48	2.50	0.35	34	2.81**
Water (%)							
Y	67.7b	3.2	48				
M	59.5b	4.5	48	56.4	4.0	34	3.13**
Male mass (mg)	86.1	22.4	29	57.6	21.6	25	4.85***
Female mass (mg)	163.8	48.4	37	84.2	9.2	24	6.46***

[a] Adults weights are means per tree. All data were log transformed prior to analysis by *t* test. Samples for a and b were taken from the same tree, and differences between means were analyzed by paired *t* test; a, df = 47, t = 3.72***; b, df 47, t = 9.72***. From Baylis (1989).

**$P < 0.01$.

***$P < 0.001$

Females of *J. evagoras* accordingly use plant quality as a cue in oviposition. Mated females placed in a cage containing plants that had been treated with fertilizer and plants that had not preferred to lay egg batches on the former (Baylis and Pierce 1991a).

Presumably because of the extreme dietary demands of ant association, lycaenids are likely to be able to respond not only to intraspecific variability in host plant quality, but to variability between individual plant parts, as well as to differences between species. Lycaenids are well known for feeding on nitrogen-rich, or water- and nitrogen-rich parts of plants such as flowers, terminal foliage, buds, shoots, and seed pods, although the degree to which this behavior correlates with myrmecophily is not known (Mattson 1980; Robbins and Aiello 1982; Thomas 1985; Milton 1990). However, larvae of the North American species, *Glaucopsyche lygdamus,* are more attractive to ants when feeding on seed pods of their legume host plants than when feeding on other parts of the plant (Pierce and Easteal 1986). Moreover, larvae of the European species, *Polyommatus icarus,* were more attractive to ants when reared on several species of herbaceous Fabaceae than on foliage of the tree *Robinia pseudacacia* (Fiedler 1990a). Fiedler points out that the relative stability of the interaction must therefore be mediated in part through the host plant.

A comparison of the food plants of 297 lycaenid species revealed that ant-tended lycaenids are more likely to feed on legumes, nitrogen-fixing nonleguminous plants and mistletoes than are their untended counterparts (Pierce 1985). An accurate evaluation of the extent to which particular ecological factors may have given rise to this pattern is impossible in the absence of a phylogeny for the group. Nevertheless, it is tempting to conclude that ants have been of central importance in shaping the host plant preferences of myrmecophilous lycaenids: legumes and nitrogen-fixing nonleguminous plants can convert atmospheric nitrogen to ammonia, which can subsequently be assimilated by the plant. These plants may thus be considered nitrogen-rich, or at least less variable in their nitrogen content over time because of their dependency on the relatively invariable atmospheric nitrogen level than on the variable soil nitrogen level. In addition, legumes frequently have extrafloral nectaries that attract ants and can act as a source of moisture for larvae (Pierce 1985; Baylis 1989). Similarly, mistletoes, which are parasitic and accordingly able to absorb selectively high quality nutrients from their host trees, may be more stable in their nitrogen and water levels than their hosts (Pierce 1985; Baylis 1989).

Conclusions

Mutualistic associations with ants have imposed several constraints on the dietary choice of the Lycaenidae. First, to obtain protection from ants, lycaenids must live in, or near to, ant-foraging trails or nests. Second, the secretion of often considerable amounts of aqueous proteins to ants, which can exact a considerable cost to larval growth, makes these nutrients of special importance in the diets of lycaenids. Severe nutritional requirements are likely to have led to the predilection, among herbivorous lycaenids, for nitrogen- and water-rich food plants such as legumes, and for the nitrogen- and water-rich parts of those food plants. These dietary preferences, coupled with the proximity of ants and ant-tended homopterans, may have facilitated the shift among some species to nectar feeding and to carnivory (Hinton 1951; Cottrell 1984).

Although myrmecophily imposes certain constraints on lycaenid foraging patterns, it may also act to diversify the range of possible diets. Ant-dependent oviposition has been frequently observed in myrmecophilous lycaenids, and this may encourage a high rate of host plant shifting. This, in turn, might be expected to promote polyphagy among myrmecophilous lycaenids, and may have been an important mechanism generating the startling diversity of diets consumed by extant species of Lycaenidae today.

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