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LYCAENID BUTTERFLIES AND ANTS: SELECTION FOR NITROGEN-FIXING AND OTHER PROTEIN-RICH FOOD PLANTS

The larvae of many species in the butterfly family Lycaenidae associate with ants. It has been shown for a number of these species that attendant ants protect larvae against parasitoids and predators, and in return, the larvae secrete food for the ants in the form of carbohydrates and amino acids (Pierce and Mead 1981; Pierce 1983). In this paper I describe how ant associations may have influenced the host-plant choices of lycaenid butterflies. In particular, I investigate whether ant-tended lycaenids are more likely to feed on nitrogen-fixing and other protein-rich plants than their untended counterparts. Myrmecophilous lycaenids have the double nutritional burden of meeting their own developmental requirements as well as secreting amino acids for attendant ants. Accordingly, one might expect selection to favor those species whose larvae feed upon protein-rich plants. Just as some unpalatable butterflies specialize on host plants containing toxic secondary compounds that provide them with a chemical defense mechanism (e.g., Ehrlich and Raven 1964; Brower and Brower 1964), ant-tended lycaenids may specialize on food plants that allow them to attract ant guards.

Lycaenidae account for about 40% of all butterfly species (Vane-Wright 1978). Although there is a rich anecdotal literature on lycaenid-ant interactions (see Hinton 1951 for review), the ecological significance of myrmecophily in the Lycaenidae has only recently begun to receive attention (e.g., Atsatt 1981; Cottrell 1983). Downey (1962*b*) noted that of 833 species whose life histories were known, 245 had been recorded as associating with ants. Ants are such an important feature in the life history of some lycaenids that females use them as cues in oviposition (Pierce and Elgar 1985). Predation and parasitism of the immature stages of the Australian lycaenid *Jalmenus evagoras* are so intense that populations of this butterfly deprived of their attendant ants cannot survive (Pierce 1983).

The larval and pupal secretions of *J. evagoras* contain high concentrations of at least 14 different free amino acids (Pierce 1983; N. Pierce, P. Rogers, and P. Vowles, in prep.). These secretions are produced by specialized exocrine glands (Malicky 1969; Kitching 1983); they are not an excretion as is the honeydew of homopterans (e.g., Way 1963). The most abundant amino acid produced by *J. evagoras*, serine, occurs in concentrations of approximately 50 mM, which is at least an order of magnitude greater than that of amino acids found in most extrafloral nectars, and is comparable to concentrations found in the salivary glands of many social insects (Maschwitz 1966; Hunt et al. 1982). Radioactive-labeling experiments and bioassays with synthetic mixtures confirmed that the amino acids secreted by both the larvae and pupae are an extremely attractive food source for workers of the attendant ant species, *Iridomyrmex* sp. 25 (Australian National Insect Collection, *anceps* group; Pierce 1983). It is likely that

secretion of amino acids as ant rewards is a widespread phenomenon among the Lycaenidae. Maschwitz et al. (1975) found methionine and simple sugars in the secretions of *Lysandra hispana*, and all of the other lycaenids that have been examined (including *Glaucopsyche lygdamus*, *Hypochrysops ignitus*, and *Ogyris genoveva*) exude amino acids from epidermal glands (Pierce 1983).

Because lycaenid larvae produce amino acids as well as carbohydrates for attendant ants, I suspected that myrmecophilous lycaenids might have a particular preference for protein-rich food sources. Lycaenids are distinctive as a taxonomic group because of their predilection for nitrogen-rich plant parts such as flowers, seed pods, and terminal foliage (Mattson 1980; Robbins and Aiello 1982). Furthermore, many lycaenids feed on nitrogen-fixing plants such as legumes. There are at least two reasons why nitrogen-fixing plants might be considered protein-rich relative to other plants. First, both the seeds (e.g., VanEtten et al. 1963, 1967) and the leaves (e.g., Akeson and Stahman 1966) of legumes have been found to contain among the highest percentages of protein of all plants that have been sampled. Second, plants that fix nitrogen may exhibit less temporal variation in their protein content than plants that require nitrogen sources in the soil. The latter are subject to fluctuation depending upon nitrogen availability in the substrate, whereas plants with nitrogen-fixing symbionts are not.

At least eight angiosperm families other than legumes possess root-nodulated nitrogen fixation (Becking 1977; Torrey 1978), and several are known to contain blue-green algae as stem symbionts (Silver 1977). In addition to these angiosperms, members of the Cycadaceae, Strangeriaceae, and Zamiaceae have nitrogen-fixing associations with blue-green algae (Grobbehaar et al. 1971; Becking 1977; Silvester 1977). Certain of the lichens that possess Cyanophyta as the photosynthetic symbiont are also nitrogen-fixing, and analyses of the nitrogen content of their leaves have shown that they are richer in total nitrogen than those species that associate with non-nitrogen-fixing, green algal symbionts (Rundel 1978). Lycaenids from Australia, South Africa, and North America have been recorded to feed on most of the known nonleguminous, nitrogen-fixing plant families. Their food plants include several species of Cycadaceae, and almost all of the phytophagous Lipteninae are specialized lichen feeders.

A number of ant-tended lycaenids that do not eat nitrogen-fixing hosts are specialized to feed on mistletoes. As plant parasites, mistletoes (and other epiphytic parasites, such as those in the families Santalaceae and Convolvulaceae) may function in a manner similar to nitrogen-fixing plants with regard to protein variability. For example, Urness (1969) noted that mistletoes exhibited only slight seasonal variation in protein content compared with other forage plants. Some plant parasites, such as *Cuscuta campestris*, are capable of extracting as much as a fourth of the total nitrogen of their hosts (Misra and Saxena 1971c). Greenham and Leonard (1965) examined four species of mistletoes and found that they were richer in free and bound amino acids than their hosts, and Nicoloff (1923, cited in Gill and Hawksworth 1961) likewise found that the two mistletoes he studied contained higher concentrations of total nitrogen than their hosts. In contrast, Misra and Saxena (1971a, 1971b, 1971c) measured considerable variability in the compositions and concentrations of different free and bound amino acids of three

epiphytic parasites and their hosts, but found no marked qualitative differences between them.

DESCRIPTION OF ANALYSIS

To test whether myrmecophily in the Lycaenidae is correlated with a protein-rich plant diet, I compared the incidence of ant attendance among species of lycaenids that feed on different kinds of plants. In particular, I examined whether lycaenids that feed on legumes are more likely to associate with ants than lycaenids that feed on other kinds of plants. To identify possible phylogenetic bias in the distribution of the traits I was examining, I analyzed the data separately by species and genera, and within the two main subfamilies represented by the sample. Finally, I assessed the occurrence of myrmecophily among lycaenids recorded as feeding on nonleguminous nitrogen-fixing plants and on mistletoes.

The data that I used for this comparative study were based on life histories of lycaenids from three geographic regions where reliable records of both food plants and ant associations are readily available: Australia (Common and Waterhouse 1981); South Africa (Clark and Dickson 1971; Claassens and Dickson 1980; and Henning 1983); and North America (Howe 1975; Downey and Allyn 1979; Dornfeld 1980; and J. C. Downey, personal communication). Only phytophagous lycaenids were considered in the analysis, and a species was regarded as tended if its larvae had ever been observed associating with ants. Records of host plants included species that supported larval growth to maturity; reports of oviposition not substantiated by subsequent observations of larval survival were discarded. A lycaenid was called a legume feeder if at least half of its recorded food-plant families are leguminous. A genus was considered ant-tended and feeding on legumes if 50% or more of its species associate with ants, and 50% or more of the total host-plant families consumed by the species within the genus are leguminous. Similarly, a lycaenid was recorded as feeding on nonleguminous nitrogen-fixing plants if at least half of its food plants belong to genera for which nitrogen fixation has been confirmed (see earlier references), and feeding on mistletoes if at least half of its food plants belong to the Loranthaceae or Santalaceae.

RESULTS AND DISCUSSION

In all three geographic regions, the larvae of lycaenids that feed on legumes are much more likely to associate with ants than the larvae of lycaenids that feed on other kinds of plants (table 1). Similarly, among lycaenids that feed on nonleguminous nitrogen-fixing plant genera, a significantly greater proportion are myrmecophilous compared with those species that feed on other kinds of plants (table 2). Among the latter, ant attendance is correlated with diet for those species that feed on mistletoes (table 3). It is important to note, however, that most of the ant-tended species from table 3 that feed on mistletoes belong to the single Australian genus *Ogyris*, and hence it is possible that the observed correlation primarily reflects phylogeny rather than ecological similarity in this group.

The association between myrmecophily and protein-rich diet appears to be

TABLE 1

ASSOCIATION BETWEEN ANT ATTENDANCE AND CONSUMPTION OF LEGUMES IN 297 SPECIES, 86 GENERA, AND 2 SUBFAMILIES OF PHYTOPHAGOUS LYCAENIDAE FROM AUSTRALIA, SOUTH AFRICA, AND NORTH AMERICA (percentages in parentheses)

	TOTAL	RELATIONSHIP WITH ANTS		χ^2
		Tended	Not tended	
Lycaenid species				
Legume feeders	83	55(66)	28(34)	28.46
Other plant feeders	214	69(32)	145(68)	$P < .005$
Lycaenid genera				
Legume feeders	23	15(65)	8(35)	5.63
Other plant feeders	63	23(36)	40(64)	$P < .03$
Lycaenid subfamilies				
Theclinae				
Legume feeders	37	29(78)	8(22)	12.96
Other plant feeders	119	53(45)	66(55)	$P < .005$
Polyommatinae				
Legume feeders	46	26(56)	20(44)	14.80
Other plant feeders	73	16(22)	57(78)	$P < .005$

TABLE 2

ASSOCIATION BETWEEN ANT ATTENDANCE AND CONSUMPTION OF NONLEGUMINOUS, NITROGEN-FIXING PLANTS IN THE LYCAENIDAE (percentages in parentheses)

	TOTAL	RELATIONSHIP WITH ANTS		χ^2
		Tended	Not tended	
Nitrogen-fixing plant feeders	16	9(56)	7(44)	4.56
Other plant feeders	198	60(30)	138(70)	$P < .05$

NOTE.—The 214 species in the table are those species from table 1 that do not feed predominantly on legumes. For tended species, the represented food-plant families and genera are Casuarinaceae (*Casuarina*), 1; Myricaceae (*Myrica*), 1; Zygophyllaceae (*Zygophyllum*, *Tribulus*), 7. For untended species, the food-plant families and genera are lichen (with Cyanophyta), 1; Rhamnaceae (*Ceanothus*), 1; Rosaceae (*Purshia*), 1; Ulmaceae (*Trema*), 1; Zamiaceae (*Zamia*), 2; Zygophyllaceae (*Zygophyllum*), 1. Numbers are the recorded number of lycaenids feeding on each family.

TABLE 3

ASSOCIATION BETWEEN ANT ATTENDANCE AND CONSUMPTION OF MISTLETOES IN THE LYCAENIDAE (percentages in parentheses)

	TOTAL	RELATIONSHIP WITH ANTS		χ^2
		Tended	Not tended	
Mistletoe feeders	26	14(54)	12(46)	7.85
Other plant feeders	172	46(27)	126(73)	$P < .01$

NOTE.—The 198 species in the table are those from table 2 that do not feed predominantly on nitrogen-fixing plants.

generally distributed throughout the Lycaenidae. If the data are analyzed either by genera or within each of two subfamilies, the pattern remains the same as that shown by the species analysis (table 1). This result is consistent with the generally accepted viewpoint that myrmecophily is a primitive feature in the Lycaenidae and, in those species in which it is not found, has probably been lost secondarily (e.g., Hinton 1951; Malicky 1969; Fukuda et al. 1978). The 297 species from Australia, South Africa, and North America represent four subfamilies of the Lycaenidae (*sensu* Eliot 1973; cf. Ehrlich 1958), the Theclinae, Polyommatinae (= Plebejinae), Lycaeninae, and Lipteninae. None of the species from the Lycaeninae or Lipteninae in table 1 associate with ants, and therefore have not been analyzed separately in the table. The Lycaeninae from table 1 include 14 species from North America and 2 from South Africa, and the Lipteninae include 6 species from South Africa. Since both of these subfamilies are known to have myrmecophilous members in other geographic regions (e.g., Hinton 1951), I have retained them in the sample. Their omission from this comparative study would not change the conclusions.

There are 46 remaining species that do not feed predominantly on either legumes or other protein-rich plant families, but are nevertheless tended by ants (see table 3). Many of these feed exclusively on nitrogen-rich parts of their host plants, such as flowers and seed pods. Ten of these species feed on legumes, but were not scored as legume feeders because leguminous families constitute less than 50% of their total host-plant families.

Plant features in addition to the nutritional ones discussed here doubtlessly have been important in the evolution of host-plant use by the Lycaenidae, and there are alternative explanations for the patterns shown in tables 1–3. For example, myrmecophilous lycaenids may lack the proteases necessary to digest complex plant proteins, and instead may rely upon the abundant free amino acids and simple soluble proteins available in protein-rich plants. It is possible that lycaenids extract specialized compounds other than proteins from nitrogen-fixing plants and mistletoes that they use in attracting ants. The association between myrmecophily and diet also may be simply a secondary effect. Extrafloral nectars are particularly rich in amino acids, and Baker and Baker (e.g., 1973*a*, 1973*b*; 1976) have suggested that their high nutritional content is an adaptation to attract foraging ants. Protein-rich plants such as legumes may be better able to afford extrafloral nectaries than other plants. These extrafloral nectaries might have then attracted ants and, with them, lycaenids.

The correlation between diet and ant attendance within the Lycaenidae is sufficiently strong that the food choices of myrmecophilous lycaenids might serve as useful indicators of nitrogen-fixing or other protein-rich plants in the environment. Apart from the nitrogen-fixing plants cited previously and mistletoes, there are a number of plant families particularly favored by ant-tended lycaenids that might warrant further investigation. In North America, the seed caps of *Nolina* (Agavaceae) are utilized by 2 myrmecophilous species. In Australia and South Africa, 11 different myrmecophilous lycaenids feed on members of the Sapindaceae. It has been recorded that 8 lycaenid species consume members of the Verbenaceae, and another 8 have been found on species of Myrtaceae. Four

lycaenids can be found on species of Anacardiaceae and four on species of Crassulaceae.

As early as 1878, while describing the larval secretions of *Celastrina (Lycaena) pseudargiolus*, Edwards (1878, p. 8) noted, "it is probable that the quality of this . . . secreted fluid . . . and perhaps its attractiveness depends on the nature of the food plant." Downey (1962a) stressed that symbiotic associations with ants might have had an important effect in shaping the food-plant preferences of lycaenids, and Atsatt (1981) highlighted variables such as the predictability of ant resources and the apparency of plants in determining lycaenid host-plant choice. Because myrmecophilous lycaenid larvae secrete amino acids as rewards for their attendant ants (Pierce 1983), I suspected that protein would be a particularly important feature of their diet. The results of this study demonstrate that among the Lycaenidae, ant association is highly correlated with the consumption of nitrogen-fixing plants and mistletoes. With the present evidence, the simplest explanation for this pattern is that these plants, more than others, can supply sufficient protein to enable the larvae to attract and maintain a retinue of ant guards.

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