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**COOPERATION VS EXPLOITATION: INTERACTIONS BETWEEN
LYCAENID (LEPIDOPTERA: LYCAENIDAE) LARVAE
AND ANTS**

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ABSTRACT

The larval stages of many lycaenid species are myrmecophilic, i.e. they are associated with ants. We revised the literature and categorized these associations as neutral (non existent, commensalistic), cooperative (mutualistic, mutualistic inquiline), and parasitic (food competitor, cleptoparasitic, predaceous symphile or synechthran). The relationships were also noted as being facultative or obligate. We suggest that the lack of evidence for a “reverse evolution” from obligatory to facultative relationships may be explained by the theory of negentropy. Within several of the lycaenid taxa there has been a change in the diet from phytophagy to aphytophagy associated with a change from cooperative to exploitative behavior towards ants. A relatively low number of species, however, seem to have followed the route from cooperative (mutualists) to exploitative behavior (cleptoparasites, predaceous symphiles, synechthrans) even though the latter may give higher returns for less investment. Even neutral behavior (no relation with ants, commensals) is more probable than exploitative behavior. We suggest that this pattern reflects both the constraints produced by the species specific nature of exploitative interactions and the stability of cooperative interactions in evolutionary terms.

INTRODUCTION

Many species of Lycaenids are myrmecophilic, i.e. they are associated with ants. Through these associations with ants, lycaenid larvae have developed a number of morphological and behavioral adaptations. Many species of larvae have evolved what have been termed myrmecophilous organs, one of the most important of these being the nectary organs which are found on the seventh abdominal segment and secrete a substance containing sugars and amino acids when solicited by the ants (Malicky, 1970; Maschwitz *et al.*, 1975; Pierce, 1983).

Apart from their morphological adaptations lycaenid larvae are unusual with respect to their diet. They may feed on lichens, homoptera or ant brood rather than on angiosperms, which is the normal food of Lepidopterous

larvae. Many of the interactions involving lycaenid larvae and ants have been described (Kitching, 1987; Fiedler and Maschwitz, **op. cit.**; Elmes *et al.* 1991) and an exhaustive revision of these was undertaken by Fiedler (1991b). Lycaenid/ant interactions have been classified as mutualistic/ parasitic, facultative/ obligate and phytophagous/ aphytophagous. Although some authors, for example, Henning (1983) have given finer classifications, the full range of possible associations have not been taken into account, for example, *Maculinea* spp. and *Liphrya brassolis* are both classed as “parasites” even though they have completely different relations with their ant hosts at a behavioral level which implies different evolutive pathways towards each of these two types of relation; *Maculinea* spp. are attended or ignored by the ants whilst *Liphrya brassolis* is attacked.

Several authors have studied the relative importance of cooperation vs exploitation using different models and have shown that in theory, “cooperation rather than exploitation dominate in the Darwinian struggle for survival” (Nowark and May 1992, Nowark *et al.* 1996, Sigmund 1992). Empirical evidence suggests that in the Lycaenidae this dominance of cooperation over exploitation may be true. Using data in the literature, most of it summarized by Fiedler (1991a,b), on the types of interactions between lycaenid larvae and ants, the myrmecophilous organs on the lycaenid larvae, the degree of relationship (facultative or obligate) and the diet of the larvae, we tentatively propose a more detailed classification of ‘types of interaction’. In each case we noted the presence or absence of the nectary organs, larval diet (spermatophytes, algae, lichens; homoptera; ants; homoptera honeydew; ant regurgitation's) and type of interactions with ants. Using this information we classified eight types of interactions the larvae may have with the ants. We then use this classification to describe the diet changes that have occurred both between and within subfamilies (from phytophagy to aphytophagy) and discuss these diet changes in the context of the relative importance of cooperative/exploitative behavior of the larvae towards their ant partners.

Types of interaction between lycaenid larvae and ants

The range of types of relationships that the ants may share with Lycaenids were classified as follows. It must be emphasized that these are “types of behavioral interactions”, not “types of larvae”. Thus a larva that is mutualistic at one stage of its life cycle may be parasitic at another. A parasitic larva such as *Maculinea rebeldi* or *M. alcon* may be generally regurgitation feeders (cleptoparasites) but during times of food shortage may also prey on eggs and ant brood (Elmes *et al.* 1991)

1. Relationship not recorded: Larvae which have unknown relationships with ants. (Relationships recorded with a question mark by Fiedler (1991a,b)).

2. Neutral relationships: The ants neither gain nor lose from the interaction with the Lycaenid larvae. The larvae, however, may neither gain or lose (No relationship) or may gain (Commensal) from the relationship.

2.1 No relationship: The larvae do not interact with ants mutualistically, parasitically or commensally. Thus neither the ants nor the larvae gain from the relation. The larvae may avoid encounters with ants using specific defensive tactics such as *Eumaeus atala* (Bowers and Larin 1989) or they may be rarely found by ants. The point is that they do not enter into ant-inhabited "enemy free space" (Atsatt 1981). In the Curetinae, and some species in the Lycaeninae, ants sometimes encounter larvae and then lick up plant sap at feeding damage. There is no evidence, however, that the larvae benefit from the relation.

2.2. Commensalistic: In these associations, unlike the "No relationship" associations, the larvae benefit from the relation, whilst the ants remain unaffected. Thus they gain a two-fold advantage (avoidance of ant attacks and entering into "enemy free space"). Commensalistic relations have been described from the subfamily Liptenini where the larvae are strictly associated with ant columns on tree trunks where they feed on lichens or algae (Downey, 1962; Atsatt, 1981a; Callaghan, 1992). The larvae supposedly gain from the relation in that the presence of ants reduces attacks from predators and parasites (Atsatt 1981a) whilst the ants remain unaffected since the larvae do not compete in any way with food or other resources. Nonetheless, Callaghan (1992) described larval behavior in 12 species from the tribe Liptenini where the larvae seem to have strictly defensive relationships with ants, thus suggesting that the ants may not be protective elements in this case and that the relationship between them and the larvae is antagonistic rather than commensalistic. There are also certain species in the Lycaeninae that can be classed as being commensalistic owing to the fact that they are or appear to be associated with ants, but apparently do not possess a nectary organ and thus presumably do not provide the ants with a substantial food resource, for example *Aloeides dentatis* (Henning 1983).

3. Mutualistic (Cooperative): This follows the standard definition of mutualist in the literature whereby both the ants and the lycaenid larvae benefit from the association. The larvae secrete a sugary nectar which the ants imbibe. The ants in return protect the larvae from predators and parasites (Pierce and Mead, 1981; Pierce et al., 1987; Baylis and Pierce, 1991) Under this definition a larva is mutualistic if it has a functional nectary organ, if the diet is phytophagous and if it is associated with ants. Mutualists may be facultative or obligate, where the term obligate is defined as complete dependency on a specific genus of ants (Fiedler, 1991b, 1994). Mutualists as defined here are only found in the Lycaeninae, Table 1.

4.1. Mutualistic inquiline: Here we define a new type of interaction which is really only a sub-division of the mutualists. In this case the larvae are attended by ants as for the mutualists, but furthermore they shelter either in

pavilions constructed by the ants or in the ant nests themselves. The larvae, however, remain phytophagous, leaving the shelters to feed on their hostplant. Examples of species which exhibit “inquiline behavior” are *Anthene emolus* (Fiedler and Maschwitz 1989) and *Paralucia aurifera* (Cushman *et la.* 1994). It must be emphasized once again that it is the interaction that is important not the species. Thus “inquiline behavior” may be a rare occurrence in a species or a life history trait. The importance of this category is that it suggests a possible intermediate stage between free living mutualists and parasites which live in the ante, lony and feed on the ant brood.

4. Parasitic (Exploitative)

In these cases the lycaenid larvae benefit from the association whilst the ants are disadvantaged. We divided the parasitic larvae in four sub-groups; food competitors, cleptoparasites (after Holldobler and Wilson, 1990), predaceous symphiles and synechthrans (after Wasmann 1894).

4.1 Food competitors: Here we define a type of interaction in which the larvae feed on homoptera (and homoptera secretions) which have a trophobiotic relationship with ants such as many species from the Miletinae (Kitching, 1987). This definition differs from that of Maschwitz and Fiedler (1988) who defined homopterophagous lycaenid larvae as ‘indirect parasites’. We suggest, however, that “food competitors” is a more precise definition. The food competitors may be further divided into ‘stealthy competition’, which are not tolerated by the ants and feed inside shelters or cover themselves with bits of their prey to protect themselves from ant attack, for example, *Spaglis* spp., and ‘symphylic cleptoparasites’, which are ignored or even sometimes attended by the ants, for example, *Miletus* spp. (Cottrell 1984, Fiedler, 1991b).

6.1 Cleptoparasites: The larvae are food robbers (*Euliphyra* spp.) or feed on oral regurgitation's from ants. Oral regurgitation feeders may be either free-living (*Spindasis takatonis*) or may inhabit the nests of the ants (*Niphranda fusca*) (Cottrell, 1984). Fiedler (1991b) defined ant regurgitation feeders as ‘parasites’, nevertheless Holldobler and Wilson (1990) define ‘food robbers’ which rob the ants of a food resource and the regurgitation feeders which receive nutrients that would normally be destined for the ant brood (oral regurgitation's) as cleptoparasitism (cleptobiosis in their terms). Cleptoparasitic behavior has been reported from both the Lycaeninae and Miletinae.

6.2 Predaceous symphile: The larvae spend all, or part of the larval phase inside the nests of their host ant, feeding on the ant brood. By means of putative pheromone secretions the larvae are accepted by the ants as their own brood whilst they (the larvae) remain in the ant nest . (Jackson, 1937; Cottrell 1984; Thomas *et. al.*, 1989). This definition applies to lycaenids such as *Maculinea arion*, *M. teleius* and *Lepidochrysops* spp., described simply as ‘parasites’ in the literature, for example Cottrell, 1984; Elmes *et al.* 1991).

6.3 Synechthran: (following Wasmann, 1894). These species of lycaenid also feed on ant larvae, but their relation with the ants has a completely different behavioral base than that of the predaceous symphiles. The larvae are not

welcome guests in the ant nests; rather they are treated as intruders, and attacked by the adult ants, such as is the case of *Liphyra brassolis* (Johnson and Valentine, 1986).

Changes in the diet within subfamilies

Changes in the diet within a subfamily have taken place in the Lycaeninae from angiosperms to ant-brood, homoptera and regurgitation's from ants, and in the Miletinae from homoptera, to honeydew, ant-regurgitation's or ant brood.

a. Changes in the diet in the Lycaeninae (all examples taken from Fiedler (1991b) unless otherwise stated.

Within the Aphaenini, Theclini and Polyommatini there has been a change in the diet from phytophagy to aphytophagy, the aphytophagous larvae feeding on homoptera (food competitors) or oral regurgitation's from the ants (cleptoparasites) but sometimes of cases on ant larvae or pupae (predaceous symphiles). The phytophagous species in the Lycaeninae are either commensals, mutualists, mutualisticinquilines or have no relation with ants. Their behavior towards the ants is thus neutral or cooperative. The aphytophagous species, however, all exploit their ant partners. Food competitors and cleptoparasites may be found in the Aphnaeini, (*Spindasis nyassae*, *S. takanonis*, *Axiocerses harpax* and *A. pseudozeritis*, oral regurgitations), in the Theclini (*Shirozua jonasi*, oral regurgitations) and the Polyommatini (*Niphanda fusca*, oral regurgitations, *Triclema lamias*, homoptera and *Maculinea* three spp.). These species have nectary organs and sometimes also tentacle organs (except *S. jonasi*, which has neither). There are predaceous symphiles in the tribes Theclini; *Acrodipsas cuprea*, *A. myrmecophila*, *A. illidgei* and Polyommatini; *Maculinea*, two spp. and *Lepidochrysops*, nine spp. As far as is known, all species possess a nectary organ only. Of these *Maculinea* spp. are generally specific to one species of ant, at least within the same geographical region (Thomas *et al.*, 1989), *Lepidochrysops* spp. are almost certainly species specific (Cottrell, 1984), although there is little information as regards the remaining genera, what evidence there is points to host ant specificity, (Cottrell, *op cit.*)

b. Changes in the diet within subfamilies in the Miletinae (all examples taken from Fiedler (1991b).

In the Miletinae there have been changes in the diet of the larvae from homoptera to other food sources. Although the scarcity of data on this tribe does not permit conclusions to be drawn we can state that in all cases studied the behavior of the larvae towards the ants is exploitative. In the Miletini there are three species reported to feed on homoptera honeydew *Miletus chinensis*, *Taraka hamada* and *Lachnocnema bibulus*, the latter is also reported to feed on regurgitations from ants. *Thestor* spp. (Miletini) are suspected of preying on ant brood. In the

Liphyrini *Euliphyra mirifica* and *E. leucyana* feed on oral regurgitations from ants and *Liphrya brassolis* (Liphyrini) feeds on ant brood. These species do not possess nectary or tentacle organs. Of these, *Lachnocnema* is not specific as regards the ant host, but *Thestor*, *Miletus*, *Euliphyra* and *Liphrya* are species specific.

DISCUSSION

Facultative and obligate relations in the Lycaeninae

Regarding the subfamily Lycaeninae, (Fiedler 1991b) discusses the development from facultative mutualisms to obligate relations of various types (mutualists, some inquilines, cleptoparasites, predaceous symphiles) or to a decrease in the interactions with ants (secondary myrmecoxeny). Fiedler (1991b) states that there 'is yet no evidence that a reverse evolution from obligatory towards facultative myrmecophily has ever occurred within the Lycaenidae, although such would be possible from theory'. We propose that the theory of negentropy provides a possible explanation for the lack of evidence for this "reverse evolution". This proposal assumes that the higher the order or complexity of an organism, including in the concept of complexity higher specialization's which may involve loss or simplifications of certain structures, the lower will be the probability state of the system and the longer the evolutionary time to produce the given state. Thus the further down a certain evolutionary pathway an organism finds itself the fewer available choices it will have to return back along that pathway. (Zotin and Konoplev, 1978; Jaffe, 1984; Jaffe and Hebling-Beraldo, 1993). We argue that obligate myrmecophiles are more "complex" in that they have more finely tuned adaptations in their associations with ants than facultative myrmecophiles. Thus in this case negentropy is expressed as specificity of communication with ants. For example, the predaceous symphiles are often associated with one or a few ant species, which implies the development of brood pheromone mimics, that are specific to a single (or a few closely related) ant species (Thomas *et al.*, 1989), probably from facultative relations where the larvae are attractive to many species of ant. A reversal of this trend would imply a loss of specificity and thus of complexity, which would revert and thus probably reduce the adaptive gains made in the first place. This negentropic assumption does not exclude the possibility of posterior losses as has taken place in the secondarily myrmecoxenous species, but predicts that these reversions should be rare and should have specific biological explanations.

Cooperation vs exploitation in lycaenid/ant relations

From Table 1, we may conclude that the majority of the lycaenid butterflies maintain neutral (no relationship, commensalistic) or cooperative (mutualistic) interactions with them, rather than exploitative (cleptoparasite, predaceous symphile, synechthran) ones. This fact seems remarkable considering that exploitative behavior may give higher nutrient returns for less investment to the lycaeind larvae. In subfamilies without a

nectary organ, i.e. where cooperative behavior has not appeared, table 1a, 64.4% of species show neutral behavior (no relation or commensal), representing the subfamilies Poritiinae (60 species) and Curetinae (7 species) and only 35.6% of the species show exploitative behavior (cleptoparasites or synechthrans) representing the Miletinae (37 species). In the Lycaeninae with 818 species, Table 1b, (excluding species for which no information is recorded), cooperative behavior dominates, with 70.5% of the larvae being mutualists as opposed to 3% being cleptoparasites or predaceous symphiles. In this subfamily, 26.5% of the species have no relation with ants are or commensals, showing that even neutral behavior is more likely than exploitative behavior. Finally, taking the Lycaenidae as a whole, Table 1a final column, 62.5% show cooperative behavior, 6.7% exploitative behavior and 30.8% neutral behavior towards the ants.

Thus, where cooperative (mutualistic) behavior is possible in the Lycaenidae this is the most probable evolutionary outcome, and where it is not likely, neutral behavior is more probable than exploitative behavior. The preponderance for mutualistic interactions over exploitative relations in Lycaenidae lead us to suppose that cooperation must have either a higher probability to evolve or to be maintained during evolution or both. Thus, we may postulate that cooperation is an evolutionarily more probable strategy compared to exploitative behaviors (Jaffé, 1995).

We propose different, but not necessarily contradictory, explanations for this pattern:

1- A model of cooperation between species as a stable strategy was developed by Axelrod and Hamilton (1981) using the Prisoners Dilemma game. The model or strategy "Tit for Tat" is simply one of cooperating on the first move and then doing whatever the other player did on the preceding move, in other words cooperation based on reciprocity. Axelrod and Hamilton (1981) showed that if the probability that two individuals will continue to interact is great enough then "Tit for Tat" is evolutionarily stable. Since then several authors have modeled cooperation vs exploitation using different versions of the Prisoners Dilemma and have shown that in theory, "cooperation rather than exploitation can dominate in the Darwinian struggle for survival" (Nowark and May 1992, Nowark *et al.* 1996, Sigmund 1992). Empirical evidence suggests that the Lycaenidae larvae benefit from the association (Pierce *et al.*, 1987; Robbins, 1991; Fiedler and Holldobler, 1992; Wagner, 1993) and there is evidence showing that both partners benefit (Fiedler and Maschwitz 1988, 1989, Hall Cushman *et. al* 1994). Cooperation in lycaenid/ant interactions is not necessarily, however, a fixed strategy (Bronstein 1994, Noe and Hammerstein 1994, 1995). Leimar and Axen, (1993) showed that the amount of nectar secreted by larvae of *Polyommatus icarus* varied according to the level of ant attendance and the larva's need for protection. A model of mutualism, commensalism and parasitism as evolutionary stable strategies in lycaenid/ant relations was developed by Pierce and Young (1986). This model assumes that the ants enhance both the growth rate and the equilibrium density of the larvae

by increasing the realized fecundity of individual butterflies and by increasing juvenile survival, whereas the larvae enhance the equilibrium density of the ants by increasing ant food supplies. Under these assumptions Pierce and Young (*op cit.*) were able to demonstrate that all three types of relation were evolutionary stable strategies. Nonetheless, although all three strategies are evolutionary stable, not all have the same odds of appearing during evolution and of avoiding extinction's in evolutionary history (Jaffé 1995). Jaffé (1995) has also shown that altruistic or cooperative behaviors may be evolutionary feasible, appearing due to evolutionary chaos in competition with exploitative behaviors. Furthermore, cooperative strategies possess economic advantages which decrease their probabilities of extinction and thus increase their odds of being fixed in the genetic repertoire of more species. That is, cooperation is a highly probable, if not necessary an evolutionary stable strategy, due to economic reasons, at least in social organisms.

2- There are three possible strategies for exploitative behavior which the larvae could take; a "synechthran" approach where the larvae fend off ant attack whilst predated on ant brood, a "stealthy" approach, whereby the larvae avoid ant attack, and a "symphilic" approach whereby the larvae deceive the ants by mimicking ant brood. Thus, ants either ignore the larvae or attend them as they predate on homoptera or ant brood. Examples of the first approach could be *Liphrya brassolis* which has an armor shaped carapace in order to withstand ant attack. This type of defense does not, however, seem to have developed in lycaenid taxa other than the Liphyrini. Examples of the second "stealthy" approach may be found in the genera *Taraka*, *Spaglis* and *Feniseca* (Miletini) where the larvae occupy silken tents or burrows, or cover themselves with remains of their prey to avoid ant attack (Cottrell, 1984; Kitching, 1987). The third "symphilic" approach involves the development of a chemical mimicry system with the larvae mimicking their homopteran prey, adult ants or ant brood. The possibility that lycaenid larvae are chemical mimics has been studied for *Aloeides dentatis*, a non mutualistic inquiline and *Lepidochrysops ignota*, a predaceous symphile (Henning, 1983). In both species, larval epidermal glands produced a secretion that appeared to mimic the brood pheromones of the host ants, although Henning (1983) did not identify the chemical compounds involved. It is also supposed that *Maculinea* spp. mimic the brood pheromones of their *Myrmica* ant hosts (Thomas *et al.*, 1989), although chemical analyses have not been undertaken as yet. In the Miletini many lycaenid larvae such as *Miletus* spp., *Lachnocnema bibulus* are attended by ants even though they do not give any reward (Cottrell, 1984).

All of these strategies; the "synechthran" approach, the "stealthy" approach and the "symphilic" approach carry with them certain disadvantages. The carapace used by *Liphrya brassolis* may not be 100% effective against all ant species, with the larvae possibly incurring high mortality rates as a result. This thus restricts the larva to only

associating with *Oecophylla* spp. The stealthy larvae may still be attacked by ants in spite of their protective burrows. The symphiliid larvae are constrained by having to penetrate the complex chemical communication systems of ants, which are highly species specific. In this sense it is notable that the larvae mimic the brood of the ants rather than the adult ants. In the genus *Myrmica* (usually hosts for larvae of *Maculinea* spp.) the brood odor is not specific to one species and *Myrmica* brood are transferable between the nests of different species (Brian 1975, Howard *et al.* 1990), although Thomas *et al.* (1989) point out that these ants are far more discriminatory under conditions of stress.

3- As far as the "symphiliid" or "mimicry" approach to exploitative behavior is concerned, lycaenid larvae mimics are normally specific to one species of host ant (Cottrell, 1984; Thomas *et al.*, 1989), which is probably due to a specificity in the chemical signals the ants use to recognize nest companions and brood (Holldobler and Carlin, 1987). Although this species specificity of the lycaenid larvae towards their ant hosts may have led to a diversification of some genera, for example *Maculinea*, *Lepidochrysops*, this diversification is far lower than that of cooperative taxa, a finding that contradicts the hypotheses of Pierce (1984) who argued that species specificity should amplify the species diversity of the Lycaenids. Nonetheless, being associated with only one species of ant carries with it certain ecological disadvantages for the lycaenid larvae such as constraints on their distribution caused by a patchy distribution of their host ant species (Jordano *et al.*, 1992), problem of host encounter in areas with a highly diverse ant fauna, and nutritional constraints (Fiedler, 1991b). For the predaceous symphiles exploitative behavior also carries with it a high risk. Their host ants are generally tolerant of intruders in times of plenty, but when food reserves are low they become increasingly intolerant and will even eat their own brood (Thomas *et al.*, 1989). The lycaenid larvae must therefore, be under extreme pressure to mimic their hosts as closely as possible and it is thus not surprising that so few species have developed this type of relation.

4- We may speculate that parasites normally have shorter life cycles than their hosts, as for example viral or bacterial parasites on insect hosts. Thus, cooperative mechanisms are more likely to act in interactions between two species with equivalently long life cycles. As ant workers and butterflies have roughly the same life-span (around one year), exploitation of one by the other is evolutionary unlikely. The data summarized here does not seem to contradict this assumption.

In conclusion, a relatively high proportion of species seem to have stabilized their evolution to cooperative (mutualists) behavior. We suggest that this pattern reflects the stability of cooperative interactions in evolutionary terms, at least among Lycaenidae in their interactions with ants.

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Table 1. Number of species and relative proportions of neutral, cooperative and exploitative interactions found between lycaenid larvae and ants.

Table 1a. Within the subfamilies of the Lycaenidae.

Table 1b. Within the Lycaeninae.

Table 1a

Type of relation	PORITINAE		MILETINAE		CURETINAE		LYCAENINAE		
	Liptenini	Miletini	Liphryini	Curetini	TOTAL	%*		GRAND TOTAL	%*
PHYTOPHAGOUS									
Relation not recorded	0	0	0	0	0		122	122	-
Neutral	60	0	0	7	67	64.4	216	283	30.8
Cooperative	0	0	0	0	0		574	574	62.5
APHYTOPHAGOUS									
Exploitative	0	28	9	0	37	35.6	24	61	6.7
TOTAL	60	28	9	7	104	100	936	1040	100

* The last column (%) refers to the relative proportion of lycaenid larvae in a given type of interaction with ants with respect to the total number of larvae. Larvae with a 'relation not recorded' are NOT taken into account.

b

LYCAENINAE							
f relation	Aphnaeini	Lycaenini	Theclini	Eumaeini	Polyommattini	Total	%*
n not ed l	4	0	0	104	14	122	--
ative	5	38	44	101	27	215	26.5
tive	18	0	57	111	284	470	
e	49	0	19	2	34	104	
cooperative	67	0	76	113	318	574	70.5
iative	4	0	4	0	16	24	3
L	80	38	124	318	376	936	100

* The last column (%) refers to the relative proportion of lycaenid larvae in a given type of interaction with ants with respect to the total number of larvae. Larvae with a "relation not recorded" are NOT taken into account.

Fig. 1.

All lycaenids in this group are phytophagous in at least one of the larval stages.

	Phytophagous		
	NO RELATION		24.8%
	COMMENSAL		1.5%
	MUTUALIST FACULTATIVE		51.8%
	MUTUALIST OBLIGATE		11.5%
	INQUILINE		0.4%
	Aphytophagous		
	CLEPTOPARASITE		1.3%
	PREDACEOUS SYMPHILE		2.4%
With nectary organ			
COMMON ANCESTOR			
Without nectary organ	Phytophagous		
	NO RELATION		51.9%
	COMMENSAL	12.5%	
	Aphytophagous		
	CLEPTOPARASITE	35.6%	
	SYNECHTHRAN		10.6%

All lycaenids in this group are aphytophagous, or at least do not feed on angiosperms (except Curetinae).

Explanation of figures

Table 1. Phylogenetic patterns in the morphological and behavioral adaptations associated with myrmecophily in the family Lycaenidae.

Key to table 1.(for explanations see text)

Type of relationship: No relationship: X, Mutualistic: Mu, Mutualistic inquiline: In, Commensalistic: Co, Cleptoparasite: Cp, Predaceous symphile: Ps, Synethran: Sy.

Degree of relationship: No relationship: X, Facultative relationship: Fa, Obligate relationship: Ob.

Myrmecophilous organs: Nectary organs: No, Tentacle organs: To, Nectary and Tentacle organs N/T, No

organs: X.

Larval diet: Phytophagous on angiosperms - dicotyledons and monocotyledons: Ph, Fungi, algae, ferns: Fu, Lichens: Li, Homoptera: Ho, Ants: An, Homoptera and ants: H/A, Regurgitations: Re, Angiosperms and regurgitations: P/R, ants and regurgitations: F/R, homoptera and regurgitations H/R. (Downey, 1962; Ehrlich and Raven, 1965; Atsatt 1981).

Geographical distribution: Palearctic (Europe): Pa, Nearctic (North America): Ne, Asiatic: As, Australian: Au, African: Af, African and Asiatic: F/S, Asiatic and Australian: S/U.

? alone Indicates that there is no information; ? after an abbreviation indicates that the trait is probable, eg. No?; the larva probably has a nectary e ofn.

Table 2.a To show the relative percentages of lycaenid species in the different types of relationships in the subfamilies Lycaeninae, Polyommatainae and Theclinae

Table 2.b To show the relative percentages of lycaenid species in the different types of relationships in the subfamilies Liphyrinae, Miletinae, Lipteninae and Curetinae.

Table 2a

Table 2b

There appear to be several different types of relation that aphytophagous lycaenid larvae have with their ant companions. In order to disentangle these it is helpful to separate the relations into two basic types: aphytophagous larvae which spend some or all of their larval life cycle in ant nests and aphytophagous "free-living" lycaenid larvae.

Examples of the first type are *Maculinea* and *Lepidochrysops* (Polyommagini), *Oxychaeta dicksoni* and *Phasis* spp. (Aphaenini) and *Pseudodipsas illidgei* (Theclini). The inquiline *Aloeides dentatis* (Aphaenini) may be an intermediate step.

Species in the genera *Maculinea* and *Lepidochrysops* and the species *Niphhranda fusca* come under the heading of predaceous symphile. These may be further divided into predaceous symphile facultative and predaceous symphile obligatory. All the species in the genus *Lepidochrysops* and *Maculinea arion*, *M. nausithous* and *M. telius* are obligate symphiles, and *M.alcon*, *M. rebeli* and *Niphhranda fusca* are facultative symphiles. The obligate symphiles feed exclusively on ant brood and pupae whereas the facultative symphiles are not exclusive predators of the ant brood, but also receive regurgitations and bits of insect prey from their hosts. *N. fusca* is reported to be fed on oral regurgitations by the ants, no other food is mentioned (Cottrell 1984). The question here is which is the more advanced form of symphile. Elmes **et. al** (1991) suggested that the facultative symphiles

Maculinea rebeli and *M. alcon* have evolved the more advanced form because they are fed directly by the ants and because they continue to be treated as ant brood once inside the nest whilst the obligate symphiles are largely ignored by the ants once in the nest. This is supported by our data in the sense that there are far more species of obligate symphiles (12 spp.) than facultative symphiles (two spp.), table 2.0, and thus it seems reasonable to assume that the facultatives have evolved from the obligates and not the other way round. It would be interesting to gain more information on *N. fusca* in order to ascertain the treatment of the ants towards the larvae in this case.

Within the Aphaenini and Theclini there is very little information on the details of the relations. , *Oxychaeta dicksoni*, *Phasis* spp. and *Pseudodipsas illidgei* are known or thought to be aphytophagous and we have put them in the category predaceous symphile because they have been found in ant nests but there is no information about the relationships these larvae have with the ants, nor whether they possess myrmecophilous organs. An intermediary step for this type of relation could be *Aloeides dentatis* which we have classified as a mutualistic inquiline. The third to sixth instars of the larvae shelter in the ants nest during the day, leaving between 19 and 21 hours to feed on foliage and returning to the nest afterwards. During the winter months the larvae stay in the nest where they pupate. The larvae thus spend some time in the nest whilst maintaining their phytophagous habits but it is not difficult to see that given the carnivorous tendencies of the lycaenids some inquilines could have made the change to predation on ant brood.

The "free living" route has been followed mostly by species from the Aphaenini and Theclini although there is one species from the Polyommataini which also fits into this category. The Polyommataini species *Triclema lamias* has been found feeding on coccids. This larvae is presumably a mutualist since it possesses a nectary organ and is attended by ants. "Free living" aphytophagous species in the Aphaenini and Theclini come from the genera *Spindasis*, *Trimenia*, *Pseudodipsas*, *Shirozoa*, and *Zesius*.

RESULTS

The following patterns emerged:

PORITIINAE

PORITIINI: Although not included in this study there is no known association between larvae of the Poritiini and ants (Fiedler 1991b).

LIPTENINI: All records of the type of relationship were commensalistic (including possible commensalists), or no relation with ants. The larvae are strictly associated with ant columns on tree trunks where they feed on lichens (Atsatt, 1981a). There were no records of myrmecophilous organs.

MILETINAE

MILETINI: The Miletini either do not have relationships with ants, or they show cleptoparasitic or synechthran

relationships, which may be either facultative or obligate. They are all exclusively homopterophagous except for the cleptoparasites which are also reported to feed on regurgitations from ants. There are no records of any member of the tribe having either a nectary or a tentacle organ. This agrees with Kitching (1987) who suggests that the absence of the tentacle, and nectary organs is characteristic of the tribe.

LIPHYRINI: Of the records of type of relationship, five (*Aslauga* spp.) are of no relation, two are of a cleptoparasitic relation (*Euliphyra mirifica*) and the other (*Liphyra brassolis*) is a synechthran. The confirmed presence of tentacle organs in five of the *Aslauga* species is characteristic of the genus (Cottrell, 1984), otherwise there were no records of myrmecophilous organs present. The larvae are carnivorous or feed on regurgitations from ants which agrees with Cottrell (op cit.), who states that no member of the Liphyrini is thought to be phytophagous.

CURETINAE: Of the six records of *Curetis* available, only one, *Curetis regula* has been shown to have some relation with ants. The association with ants is very loose; the ants are attracted to the plant exudate at leaf tissue freshly damaged by the larvae. The larvae do, however, possess functional tentacle organs although their homology to those found in other sub-families has been questioned (Fiedler, 1991b).

LYCAENINAE:

APHAENINI: There were 28 reports of mutualisms with ants (including suspect mutualists). The four cleptoparasites have both tentacle and nectary organs and the inquiline and six suspected predaceous symphiles also have tentacle organs. *Cigaritis zohra* also has a nectary organ. The diet of this taxon is varied with its members feeding on spermatophytes, regurgitations and possibly on homoptera and ants.

LYCAENINI: All records show little or no interaction with ants corresponding with a lack of nectary or tentacle organs. The Lycaenini are all phytophagous.

THECLINI: There are 38 species with mutualistic or suspected mutualistic relations with ants, one inquiline (*Paralucia aurifera*) (Cushman **et al.**, 1994), one cleptoparasite (*Shirozua jonas*) and four predaceous symphiles (*Acrodipsas* spp. and *Zesius chrysomallus*). The mutualists by definition have a nectary organ and most species also possess a tentacle organ. The cleptoparasite, *Shirozua jonas*, has neither a nectary nor a tentacle organ. The predaceous symphiles have nectary organs (where confirmed) but no tentacle organs. The Theclini have a wide range of diet; they may feed on spermatophyta, regurgitations, homoptera or ants.

EUMAEINI: All members of this taxon are facultative mutualists or have no relation with ants or the relation is unknown. *Amblypodiiiti anita* has no relation with ants and possesses both a nectary organ and a tentacle organ. Otherwise larvae with no relation have no myrmecophilous organs. All larvae are phytophagous on spermatophyta.

POLYOMMATINI: These larvae are largely mutualists or suspected mutualists (384 species). There are 14 predaceous symphiles and two cleptoparasites, *Niphanda fusca* (oral regurgitations) and *Triclema lamias*

(homoptera). The mutualists and predaceous symphiles may be either obligate or facultative. All Polyommata in mutualistic associations with ants possess a nectary organ, or both a nectary and a tentacle organ and all predaceous symphiles possess a nectary organ but not a tentacle organ. All available records show either a phytophagous or a formicophagous diet, except for *Niphanda fusca* and *Triclema lamias.pindasis takanonis* (Aphaeni) reported as 'nibbleing' at lichen (Cottrell, 1984). Phytophagous (spermatophyta, ferns) lycaenid larvae are only found in the subfamily Lycaeninae. Most of the homopterophagous species are from the Miletinae, although there is one report from the Lycaeninae (*Triclema lamias*, Polyommata). All formicophagous species are from the Miletinae and Lycaeninae (Aphaeni, Theclini, Polyommata).

There are records of regurgitation feeders from the Miletinae (Miletini one sp., Liphyrini two three species and the Lycaeninae (Aphaeni; one species, Theclinae; one species, Polyommata; three species).here are 14 predaceous symphiles and all predaceous symphiles possess a nectary organ but not a tentacle organ. All available records show either a phytophagous or a formicophagous diet, except for *Niphanda fusca* and *Triclema lamias*.

Within the subfamilies without a nectary organ exploitative behavior seems to be more common than cooperative behavior. This is probably because the types of exploitative behavior present in this group, except synecthran, ('commensal' aphytophagous, cleptoparasite) seem to require a much lower specificity of host ant, with even species in the more advanced genera highly adapted to ants such as *Miletus chinensis* and *Lachnocema bibulus* not showing specificity even as far as genus level. In fact, only the synecthrans are specific to one species of ant (Cottrell, 1984), although for four of these, *Thestor* spp., information is scarce as regards possible hosts and indeed predation on ant brood is only suspected, Cottrell (1984) mentions that 4th instar larvae of *Thestor dicksoni* refuse ant brood.

Although the systematics of the Lyphilidae are not yet a phylogeny and many of the cladistic relationships between the taxa not yet clear, the present day classification of the Lycaenidae divides the family into four subfamilies: Poritiinae, Miletinae, Curetinae and Lycaeninae. The Poritiinae and Miletinae are both divided into two tribes; Poritiini and Liptenini, and Miletini and Liphyrini respectively and the Lycaeninae into five tribes; Aphaeni, Lycaenini, Theclini, Eumaeini and Polyommata (Scott and Wright, 1990; Fiedler, 1991b). The Poritiinae and Miletinae are generally considered the more primitive subfamilies of the Lycaenidae, the systematic position of the Curetinae is uncertain and the Lycaeninae are considered the most advanced subfamily (Fiedler, op cit.).

The relationship of ant associations to phylogeny has been discussed in general terms by Pierce (1987)

who argued that the distribution of ant association within the Lycaenidae was independent of phylogeny and instead related to the geographical location of the species of lycaenid. This view has been challenged by Fiedler (1991a) who presented evidence which demonstrated that at least within the European and North African Lycaeninae the occurrence of ant associations was closely related to Lycaenid phylogeny.

In this paper we review the literature regarding lycaenid/ant interactions worldwide, in order to investigate the distribution of ant associated organs and food use within the Lycaenidae and relate these to the established classification of this family. We do not attempt to propose a phylogeny of the family but rather to discuss the role the ant organs and diet changes may have played in different evolutionary routes taken by lycaenid larvae in their association with ants based on the present classification of the Lycaenidae (Fiedler 1991b)

Analysing the data from tables 2a and b. the following trends are evident:

All lycaenid larvae possessing a nectar organ, or a nectar and a tentacle organ are from the subfamily Lycaeninae. Lycaenid larvae with a tentacle organ only are found in the Miletinae (Liphryini), Curetinae, or Lycaeninae (Aphaenini). Lycaenid larvae with neither of these myrmecophilous organs can be found in all the subfamilies.

All lycaenids with a commensalistic relation with ants are from the subfamily Poritinae, no species has either a nectary or a tentacle organ. All lycaenids with a mutualistic relation with ants are from the subfamily Lycaeninae and

The results show that the range of types of relation both between and within sub-families is wide and varied. Nevertheless the morphological adaptations seem to form more definite patterns between subfamilies. It seems likely, then that the morphological adaptations are a product of evolutionary trends, and that these adaptations have formed the framework within which the development of the different types of relations have been shaped.

With this in mind two basic patterns can be observed which provide a certain structure to the different types of relations between the lycaenid larvae and the ants. The first pattern is that the nectary organ is normally present in most taxa of the Lycaeninae (group 1) whereas it is totally absent in the Poritinae, Miletinae and Curetinae (group 2) (Fiedler 1991b).

The appearance of the tentacle organ in the subfamilies Liphryinae and Curetinae, as well as in the Lycaeninae, Polyommattinae and Theclinae is interesting and begs the question; did this organ develop early in the evolutionary history of the lycaenids and was then subsequently lost, or did it develop separately within the different groups? Cottrell (1984) states that "in most Theclinae and in the Polyommattinae the tentacles evert directly from the body surface. In the Curetinae and Liphryinae (*Aslauga*) they arise from sclerotized basal tubes

and in the Aphaenini (Theclinae) from short, partially sclerotized tubes". This suggests that the tentacle organs may have developed separately. DeVries **et. al** (1986), however, affirm that the tentacle organs on *Curetis* (Curetinae) are homologous to those found in the Liphyrini (Miletinae), Theclini and Polyommataini (Lycaeninae). It is interesting to note that the confirmed predaceous symphiles in the Lycaeninae lack a tentacle organ. This is probably a secondary loss associated with this type of relation and can be explained by the fact that the secretions of the tentacle organ produce an "alarm" reaction in ants, thus increasing their aggressiveness towards potential predators of the larvae. Since lycaenid larvae in the parasitic stage are housed in the ants nest they do not require that the ants make extra effort to protect them from predators, and indeed an aggressive ant could well attack them. This would lead to a selection against tentacle organs in these cases.

There are three species of inquiline, *Aloeides dentatis* (Aphaenini) *Paralucia aurifera* (Theclini) and *Anthene emolus* (Polyommataini). *A. dentatis* possesses a tentacle organ only, whilst the latter two species possess both tentacle and nectary organs. This change has occurred in ten species in seven genera in the Aphaenini (*Spindasis*, *Axiocerses*, *Cigaritis*, *Oxychaeta*, *Tylopaedia*, *Trimenia*, *Argyrocupha*) four species in two genera in the Theclini (*Acrodipsas*, *Zesius*) and 14 species in two genera in the Polyommataini (*Lepidochrysops*, *Maculina*), table 2a. In some cases it occurs within a species in different instars, for example *Maculinea* spp. which are phytophagous until the third instar when they become carnivorous on the ant brood.

One of the major assumptions or hypothesis regarding the evolution of myrmecophily in the lycaenids is that myrmecophily is a primitive trait and the non-association with ants a posterior development (Hinton, 1951; Malicky, 1969; Cottrell, 1984; Kitching and Luke, 1985), although Fiedler (op cit.) argues convincingly for myrmecophily as the primitive state in lycaenids. Thus, it is supposed that the nectary organ also developed early in the history of the lycaenids and where it is not present this is due to a secondary loss (Malicky 1969, Atsatt 1981a, Scott and Wright 1990) (but see Fiedler 1991b).

We have investigated lycaenid/ant relations and classified them into seven types. These types may reflect cooperative, commensalistic or exploitative behavior. The preponderance for cooperative relations in the Lycaenidae may be related to the evolutionary stability of this strategy coupled with the fact that exploitative interactions are generally species specific which implies certain disadvantages for the lycaenid larvae whereas cooperative relationships tend to involve non-specific ant relations.