

Ants and *Polyommatus icarus* immatures (Lycaenidae) – sex-related developmental benefits and costs of ant attendance

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Summary. Third and fourth instar larvae and pupae of the facultatively myrmecophilous Palearctic blue butterfly *Polyommatus icarus* showed no alteration in developmental time when reared in the presence of two species of *Lasius* ants. Sex differences were observed in larval growth and pupal weight, with males growing larger and faster. Sex-related differences also occurred in the costs and benefits of ant-attendance. Male pupal masses tended to be larger in individuals associated with ants, and their pupal weight loss was not enhanced by ant attendance. This positive developmental effect of myrmecophily is tentatively attributed to a stimulating influence of ants on caterpillar feeding behavior. In contrast, females associated with ants tended to lose more weight during the pupal stage. Hence there is evidence for developmental benefits, rather than costs, of myrmecophily in male *P. icarus* immatures, whereas ant attendance appears to be more costly for females during the pupal stage. These findings are discussed in relation to data on other myrmecophilous lycaenid species. It is suggested that maintaining low-level myrmecophily and its related organs is a comparatively inexpensive evolutionary stable strategy among this butterfly group.

Key words: Lycaenidae – Formicidae – Myrmecophily – Mutualism – Cost-benefit analysis

The caterpillars of a large number of species of the butterfly family Lycaenidae are associated with ants. Although there is a wide range of different coexistence patterns, from simple commensalism to facultatively or obligatorily symbiotic or even parasitic associations, the majority of caterpillar-ant interactions are believed to be mutualistic: caterpillars receive from the ants protection against enemies and, in return, reward their ant guards with food. Nearly all myrmecophilous lycaenid cater-

pillars possess specialized exocrine glands (pore cupola organs and a dorsal nectary organ; e.g. Cottrell 1984; Kitching and Luke 1985) that produce nutritive secretions containing carbohydrates and/or amino acids. Ant species maintaining trophic symbioses with plants or homopterans eagerly harvest these larval secretions (Malicky 1969; DeVries 1991) and even recruit nestmates to such food sources (Fiedler and Maschwitz 1989a). In turn, the ants provide some protection against predators or parasitoids of the butterfly larvae.

However, experimental data, supporting this view are scanty. The only detailed cost-benefit studies available are those of Pierce et al. (1987) and Nash (1989) on the Australian lycaenid species *Jalmenus evagoras* (Lycaenidae: Theclini: Zesiiti) and its attendant ants belonging to the genus *Iridomyrmex*. In some myrmecophilous lycaenid species (Maschwitz et al. 1975; Pierce 1983, 1989), and in one ant-associated riodinid species (DeVries and Baker 1989), at least the main components of caterpillar secretions are known. Fiedler and Maschwitz (1988, 1989a, b) presented data on two myrmecophilous lycaenid species supporting the idea that caterpillar secretions contribute to the nourishment of ants, and many rather anecdotal observations on numerous other species (reviewed in Fiedler 1991b) agree with this hypothesis.

Although the protective effect of ant attendance has been experimentally confirmed only in the Nearctic lycaenid *Glaucopsyche lygdamus* (Pierce and Mead 1981; Pierce and Eastal 1986), some Australian *Jalmenus* species (Pierce et al. 1987; Pierce 1989; Nash 1989), and in the Neotropical riodinid *Thisbe irenea* (DeVries 1988, 1991), the available evidence clearly indicates that benefits may accrue to both partners in lycaenid-ant interactions. The ecological balance may be even more delicate in some species; in *Jalmenus evagoras*, for example, braconid parasitoids use certain attendant ants as oviposition cues (Nash 1989).

Few studies have tried to assess the costs of myrmecophily for both the lycaenid caterpillars and ants. Nash (1989) demonstrated that attending *Jalmenus evagoras* larvae and pupae poses substantial energy costs to *Ir-*

idomyrmex ants. The energetic costs for the lycaenids in the same system, on the other hand, are less clear. Pierce et al. (1987) found that ant attendance and its associated secretions constrain mass gain of *J. evagoras* during the larval period and enhance weight loss during the pupal stage. Ant-attended larvae pupate at lower weights, and attended pupae lose more weight during development, resulting in an average reduction of adult mass by 25%.

Besides this reduction in size, which is closely related to reproductive fitness costs (Elgar and Pierce 1988), larval development of *J. evagoras* was accelerated from 28.83 to 23.29 days in the presence of attendant ants, whereas pupal duration increased slightly, but significantly, from 7.54 to 7.79 days. However, Baylis (1989) observed only a minimal reduction of the duration of the first three larval instars (6.86 versus 6.58 days) and no effects on the developmental rate of later instar larvae and pupae. Hence, overall development of *J. evagoras* tends to be accelerated in the presence of ants, but the extent of this effect apparently varies with experimental conditions. Furthermore, the biological relevance of this acceleration is limited given the climatic constraints governing the seasonality and voltinism of *J. evagoras* (Nash 1989).

Robbins (in press) has provided the only other study available on developmental costs of ant attendance in the Lycaenidae (but see Henning 1984). He found that in the Neotropical species *Arawacus lincoides* (Lycaeninae: Eumaeini: Eumaeiti) ant-associated larvae pupate 0.68 days later than untended controls, but there were no effects of ant attendance on initial pupal weights.

Here we report on experiments involving the Palearctic butterfly *Polyommatus icarus* Rott. (Lycaeninae: Polyommataini: Polyommataini) and two species of the ant genus *Lasius* (Formicinae). *P. icarus* is a widespread and polyphagous lycaenid species inhabiting a variety of non-forested habitats. The larvae feed on a number of herbaceous Fabaceae genera, especially preferring inflorescences and terminal foliage, and they are often visited by ants during the third and fourth (final) instar. Published field records cover at least five ant species in four genera (Fiedler 1991b). The association with ants is, however, rather loose and facultative, and *P. icarus* was therefore scored as only moderately myrmecophilous (Fiedler 1991a), whereas *J. evagoras* and *A. lincoides* belong to the ecological categories of obligatorily and steadily ant-associated lycaenids, respectively.

Lasius niger is a common grassland ant species and has repeatedly been found visiting *P. icarus* caterpillars. However, associations tend to be unstable due to the generally rather vagrant behavior of this ant species. In the laboratory, tending behavior of *L. niger* towards *P. icarus* larvae occurred intermittently and somewhat unpredictably (Fiedler, unpubl.). *L. flavus*, in contrast, is constantly attracted to *P. icarus* caterpillars in the laboratory and maintains stable trophobiotic associations (Fiedler 1991b), although this ant species with its subterranean life habits will rarely if ever encounter *P. icarus* larvae in nature.

Our study had two aims: firstly, to examine whether ant attendance produces any developmental effects in *P. icarus* caterpillars and pupae, and secondly, to assess whether the different persistence of tending behavior of the two *Lasius* species has any effect on the caterpillars. To our knowledge, this is the first such investigation with a member of the species-rich lycaenid tribe Polyommataini, and the first example within the ecological category of loosely ant-associated species.

Material and methods

P. icarus larvae were obtained from a laboratory stock (F2 generation) reared from a female caught in the Spessart hills (central Germany). The larvae were fed inflorescences and terminal foliage of *Medicago sativa* L. (Fabaceae). Since host-plant quality appears to affect the attractiveness of myrmecophilous caterpillars (Fiedler 1990; Pierce et al. 1991; Baylis and Pierce 1991), special care was taken to standardize the food supply. Experiments started with late second instars in molt, or freshly molted third instars, i.e., at the time the dorsal nectary organ and tentacle organs of *P. icarus* become functional (Malicky 1969). Groups of ten larvae each were transferred into transparent plastic cups (120 ml) lined with moistened filter paper. Food was provided in excess. Filter paper and food were changed daily. In the experimental treatments, ten worker ants of *Lasius niger* (two replicates) or *L. flavus* (three replicates), respectively, were introduced. The ants originated from laboratory colonies. Dead ants were replaced by new workers from the same colonies if needed to ensure a 1:1 ratio of ants and larvae throughout the experiments. Identical plastic vials without ants and started exactly in parallel with sister larvae served as controls. Experiments and controls were run until adult emergence in a RUMED environmental chamber at $25 \pm 1^\circ \text{C}$ under a 16:8 h L:D regime.

The following developmental parameters were recorded: combined duration of the third and fourth larval instar (larval duration); initial pupal weight (within 16 h after pupation); growth rate (defined as the difference between initial pupal weight and the average larval weight at the beginning of the third instar (= 2 mg), divided by larval duration); final pupal weight (within 16 h prior to eclosion); absolute and relative weight loss (in per cent of initial pupal weight) during pupal stage; and duration of pupal stage. Weights were determined to the nearest 0.5 mg using a Mettler AE 200 balance. Larval and pupal duration were scored in days since the exact hours of the respective molts could not be observed in most cases. Sex determination was only possible with pupae at least 6–7 days old, when the pigmentation of the pharate adult becomes visible. The data obtained were evaluated statistically using the Mann-Whitney *U*-test for direct comparisons of two data sets or ANOVA for more complex analyses.

Results

Experiments with Lasius niger

Inspection at irregular intervals confirmed that *L. niger* ants only intermittently attended the larvae or pupae. Usually at any one time some lycaenid individuals were not visited by an ant. Larval and pupal survival were lower for tended individuals than among untended controls, but the difference was not statistically significant (with ants: 14 pupae yielding 11 adults; without ants: 18 pupae yielding 17 adults; initially 20 larvae in each treatment; χ^2 , 2 df = 4.286, $P = 0.116$; combining larval and

Table 1. Developmental parameters of *Polyommatus icarus* caterpillars and pupae in experiments with the ant species *Lasius niger*

	With ants	Without ants
Larval duration L3 + L4 (days)		
Males	12.40 ± 0.68 (5)	11.22 ± 0.36 (9)
Females	12.43 ± 0.53 (7)	13.00 ± 0.57 (8)
Growth rate L3 + L4 (mg/day)		
Males	6.24 ± 0.91 (5)	6.04 ± 0.24 (9)
Females	5.22 ± 0.37 (7)	4.97 ± 0.23 (8)
Initial pupal weight (mg)		
Males	77.00 ± 7.26 (5)	69.67 ± 3.33 (9)
Females	66.36 ± 4.17 (7)	65.81 ± 1.82 (8)
Final pupal weight (mg)		
Males	68.00 ± 6.24 (5)	60.11 ± 2.84 (9)
Females ^a	53.42 ± 3.29 (6)	57.25 ± 1.68 (8)
Pupal weight loss (mg)		
Males	9.00 ± 2.69 (5)	9.56 ± 1.13 (9)
Females	10.50 ± 0.94 (6)	8.56 ± 0.58 (8)
Relative pupal weight loss (%)		
Males	11.37 ± 3.12 (5)	13.57 ± 1.30 (9)
Females ^b	16.36 ± 0.89 (6)	13.01 ± 0.80 (8)
Pupal duration (days)		
Males	8.00 ± 0.00 (5)	7.33 ± 0.24 (9)
Females	7.67 ± 0.33 (6)	7.88 ± 0.23 (8)

Means ± 1 SE (numbers of individuals in parentheses)

^a One female died before completion of pupal development^b Significant difference between treatments (Mann-Whitney U-Test: $U=6$, $P<0.02$)**Table 2.** Statistical evaluation of experiments with *P. icarus* and *L. niger* (ANOVA)

	Sex	Ant attendance	Interaction
Larval duration	$F=2.906$ $P=0.097$	–	$F=2.726$ $P=0.108$
Growth rate	$F=6.326$ $P=0.018$	–	–
Initial pupal weight	$F=3.275$ $P=0.079$	–	–
Final pupal weight	$F=6.588$ $P=0.016$	–	$F=2.975$ $P=0.094$
Pupal weight loss	–	–	–
Relative pupal weight loss	–	–	$F=3.261$ $P=0.080$
Pupal duration	–	–	$F=2.986$ $P=0.094$

Only significant figures (F and p values) are given; –: no significant effect ($P>0.20$)

pupal mortality: χ^2 , 1 $df=2.976$, $P=0.081$). The sex ratios with and without ants were in good accordance with the expected 1:1 distribution. There was no significant effect of ant attendance on any of the parameters recorded with the exception of enhanced relative pupal weight loss in ant-associated females (U -test, $P<0.02$).

In contrast, male growth rate was higher, larval duration was shorter in males, and male pupae were larger than those of females. These sex differences were consistently observed in experiments (with ants) as well as controls (without ants). Absolute and relative pupal weight loss, and pupal duration were independent of sex (see Tables 1 and 2).

With four parameters (larval and pupal duration, final pupal weight, relative pupal weight loss) ANOVA indicated a possible interaction between ant attendance and sex (Table 2). This could suggest a sex-specific differential cost-benefit balance, but interpretation is limited due to the small sample sizes and considerable individual variation.

Experiments with *L. flavus*

As expected from earlier observations, *L. flavus* ants attended the caterpillars much more persistently, and only rarely was a larva or pupa seen without an associated ant. Larval and pupal mortalities were similar with (15 pupae yielding 10 adults) and without ants (17 pupae yielding 15 adults; initially 30 larvae in each treatment; χ^2 , 2 $df=2.429$, $P=0.297$; combining larval and pupal mortality; χ^2 , 1 $df=1.714$, $P=0.188$). However, overall mortality in experiments and controls was significantly higher than in the experimental and control series involving *L. niger* (χ^2 , 1 $df=4.86$, $P<0.05$). The sex ratio was strongly male-biased in both experiments with *L. flavus* (9:3) and in the respective controls (14:3) (see below). Therefore, the subsequent analyses only consider males.

There was no evidence that ant attendance had an effect on larval or pupal duration, larval growth rate, and absolute weight loss of male pupae. However, males reared in association with *L. flavus* ants pupated at higher weights and retained this lead until eclosion (Table 3). Relative pupal weight loss likewise tended to be smaller in ant-associated males.

Table 3. Developmental parameters of *Polyommatus icarus* caterpillars and pupae (males only) in experiments with the ant species *Lasius flavus*

	with ants	without ants
Larval duration L3 + L4 (days)	12.56 ± 0.82 (9)	12.00 ± 0.57 (14)
Growth rate L3 + L4 (mg/day)	7.69 ± 0.53 (9)	7.16 ± 0.29 (14)
Initial pupal weight (mg)	95.33 ± 2.57 (9)	86.64 ± 3.72 (14) ⁺
Final pupal weight (mg)	84.22 ± 2.66 (9)	74.00 ± 3.07 (14)*
Pupal weight loss (mg)	11.11 ± 1.60 (9)	12.64 ± 1.27 (14)
Relative pupal weight loss (%)	11.62 ± 1.67 (9)	14.44 ± 1.17 (14)*
Pupal duration (days) ^a	6.88 ± 0.54 (8)	7.58 ± 0.23 (12)

Means ± 1 SE (numbers of individuals in parentheses)

^a Three individuals died as pharate adults just before eclosion
Significance levels of Mann-Whitney U-test (1-tailed): ⁺: $P<0.10$, ^{*}: $P<0.05$

Table 4. Statistical evaluation of effects of ant attendance (combined data from experiments with *Lasius niger* and *L. flavus*) on male *P. icarus* (ANOVA)

	Experimental series	Ant attendance
Larval duration	–	–
Growth rate	$F=7.779$ $P=0.009$	–
Initial pupal weight	$F=17.21$ $P<0.001$	$F=3.544$ $P=0.066$
Final pupal weight	$F=16.91$ $P<0.001$	$F=6.117$ $P=0.018$
Pupal weight loss	–	–
Relative pupal weight loss	–	–
Pupal duration	–	–

Only significant figures (F and P values) are given; –: effect not significant ($P>0.2$)

A combined analysis (ANOVA) of the data for males from series 1 (experiments with *L. niger* and controls) and series 2 (experiments with *L. flavus* and controls) revealed significant differences between these two series with regard to larval growth rate and initial and final pupal weights, whereas pupal duration, relative and absolute pupal weight loss did not differ between the two series (Table 4). In addition, pupal weights were significantly larger in the presence of ants, while all other parameters were again not significantly affected by ant attendance.

When the data for males and females from both *Lasius* species were combined, mortality was higher in experiments with ants than in untended controls (χ^2 , 2 $df=5.556$, $P=0.061$; combining larval and pupal mortality: χ^2 , 1 $df=4.858$, $P=0.026$). Given the large mortality differences between the two experimental series, this significance may be spurious.

Discussion

Development of *Polyommatus icarus*

In all treatments of our study, *P. icarus* larvae took 11–13 days to complete the last two larval instars, and the pupal stage lasted a further 7–8 days. Sex differences occurred in growth rate, size and larval duration: in *P. icarus* (as in several closely related species) males are generally somewhat larger than females and grow faster in a shorter time. This type of sex dimorphism is, however, not a universal trait among the Lycaenidae. The Australian *Jalmenus evagoras*, for example, exhibits a reverse and much more pronounced size dimorphism (Pierce et al. 1987), whereas in the Miletinae species *Taraka hamada* there is no sexual size dimorphism at all (Banno 1990).

The lead of males in larval development is in good accordance with the well-known protandry of most *Polyommatus* species, where female adults usually appear a few days later than the first males. The faster larval development of males is probably also responsible for the

male-biased sex ratio in the second experimental series employing *L. flavus*. These experiments were started 3 days earlier than those with *L. niger*, suggesting that at that time predominantly male larvae had reached the transition from the second to third instar.

Few detailed studies are available on larval development and growth parameters of other species of the large butterfly family Lycaenidae. In *J. evagoras* male pupae reach average weights of 124 or 133 mg (ant-tended and untended individuals, respectively), while female pupae average 133 mg (tended) or 165 mg (untended; Pierce et al. 1987). Although absolute pupal masses of *J. evagoras* are thus two to three times as large as in *P. icarus*, relative pupal weight losses (12–16%) and pupal duration (7–8 days) are similar in both species. However, judging from the data given by Pierce et al. (1987), larval growth rates tend to be slower in this obligatorily myrmecophilous species than in *P. icarus*.

In the Neotropical species *Arawacus lincoides* the gain in pupal weight is slightly higher (80.5–130.5 mg) than in *P. icarus* within nearly the same developmental duration (duration of the last two instars 10–12 days; Robbins in press). Accordingly, the growth rates of this typically acyclic tropical butterfly are consistently higher. Given the large systematic distance between *P. icarus* and the two tropical species *J. evagoras* and *A. lincoides*, the differences and similarities in developmental parameters allow no far-reaching conclusions. Within the Lycaenidae, body size, sexual size dimorphism, voltinism, and developmental characters are highly variable across the various taxa, and in the absence of additional data on a much larger number of species it is as yet impossible to distinguish between ecological and systematic traits. Nevertheless, although restricted to the Palaearctic region, *P. icarus* has the physiological potential for a continuous sequence of generations as indicated by the short developmental time and high growth rate.

Developmental costs of ant attendance

Our experiments yielded no clear evidence for significant developmental costs of myrmecophily in *P. icarus* caterpillars. On the other hand, a significant negative effect was the higher relative weight loss in female pupae tended by *L. niger* ants, although initial pupal weights (and thus larval mass gain) were unaffected by ant attendance. Another piece of evidence that myrmecophily is more costly for female pupae than for males might be found in the results of ANOVA. There were nearly significant interactions between ant attendance and sex affecting final pupal weight and relative weight loss, supporting the view that female pupae tend to suffer from energetic costs associated with myrmecophily.

In contrast, ant-attended males generally gained higher body masses during the larval feeding period and retained these throughout the pupal stage. This result was most pronounced in the experiments with *L. flavus*; it should be emphasized that this ant species maintained permanent associations with both *P. icarus* larvae and pupae. However, we have as yet no evidence that tend-

ing by *L. flavus* provides a significantly greater benefit for male *P. icarus* immatures than tending by *L. niger*. A combined analysis of both experimental series indicated no significant effect of ant species. Rather, ant attendance may be generally beneficial for the development of *P. icarus* males.

The mechanism underlying this unexpected observation is not clear. Possibly, ant attendance acts as a behavioral stimulus rendering the caterpillars more active and thus increasing their feeding time or motivation. In fact, many myrmecophilous lycaenid caterpillars tend to become more active in laboratory trials when ants are added (Fiedler unpublished). Furthermore, Pierce et al. (1987) have observed that in *Jalmenus evagoras* the larvae pupate 5 days earlier when associated with ants. In the aphid *Aphis fabae*, tending by *Lasius niger* ants likewise accelerates metabolism and development (Banks and Nixon 1958; El-Ziady 1960). The proximate mechanisms mediating these stimulating effects of ants towards their associated myrmecophiles require further analysis.

In both *Lasius* species the mortality of larvae and pupae was slightly, but not significantly, higher than in untended controls. Pooling all data, this difference in mortality was significant. However, this result might be an artefact, because the mortalities in both experiments and controls of the *Lasius flavus* series were almost twice as high as in the *Lasius niger* series. Therefore, it is questionable whether ant association really enhanced mortality under the rearing conditions used, whereas the mortality differences between series were significant. Unfortunately, sex determination of dead individuals was impossible for larvae and young pupae. Of the five older pupae that died prior to eclosion, three were females and two males. Thus, although a possible female-biased mortality through ant attendance cannot yet be ruled out, there is no evidence supporting this idea. In fact, as far as the causes of mortality could be ascertained, most of the larvae died from infections and a few pupae from handling effects.

Several types of developmental costs of myrmecophily have been demonstrated in the Lycaenidae. The most pronounced effects have been reported from the obligate myrmecophile *Jalmenus evagoras* (Pierce et al. 1987; Baylis and Pierce 1992). In this species the larvae and pupae must provide substantial amounts of energy-rich secretions to assure ant attendance, resulting in a significant overall reduction of adult weight and fecundity of both sexes (Elgar and Pierce 1988). In the steadily, but facultatively, myrmecophilous *Arawacus lincoides*, only a slight prolongation of larval development was found in both sexes, whereas pupal weights were independent of ant-attendance (Robbins in press). The latter author also discusses the evolutionary consequences of retarded growth due to ant attendance and concludes that myrmecophily is favored mainly in species with rather low intrinsic growth rates, or where larval mortality critically depends on the presence of ants.

Our observations with *P. icarus* provide a novel type of interaction. In this lycaenid species with its rather loose and facultative association with ants, males can achieve higher pupal weights, whereas the lack of signifi-

cant negative effects suggests that the developmental costs of myrmecophily are small for males. As has been demonstrated for at least one lycaenid species (Elgar and Pierce 1988) and several other butterflies (e.g., Wiklund et al. 1991), larger males tend to gain greater adult longevity and/or increased reproductive success. Hence, one might expect larger size and body mass to be related to increased reproductive fitness in *P. icarus* also. In particular, a sufficient lifespan is crucial for the males of this protandrous species to have a chance of mating, and the male:female interactions so common in *P. icarus* (Lundgren 1977) suggest that size alone could be an important factor.

Conversely, ant-associated females tend to lose more weight as pupae, and this should decrease their reproductive success. Thus, as in *J. evagoras*, the costs of myrmecophily are higher for females, and interestingly the relative pupal weight losses of tended females were nearly equal (c. 16%) in *J. evagoras* and *P. icarus* (Pierce et al. 1987). A possible explanation for this sex-dependent effect of myrmecophily is that females experience a more severe trade-off conflict in allocating resources to either myrmecophily or the development of their reproductive organs. This could be compensated for during the larval stage as long as the energetic investment in myrmecophily is balanced by the stimulatory effect (tended and untended *P. icarus* females achieved equal initial pupal weights), whereas in the pupae with no opportunity to gain supplementary energy this trade-off becomes obvious. In *P. icarus*, as well as in many other lycaenids (e.g., Hill and Pierce 1989), the females emerge with fully developed ovaries, usually mate on the day of eclosion, and *P. icarus* females may lay 50–100 eggs during the first 2 days of adult life (Fiedler, unpublished). Therefore, their fecundity critically depends on resources accumulated as larvae, and accordingly trade-offs between myrmecophily and fitness can be substantial.

In *P. icarus* larvae the secretion rates from the dorsal nectary organ are low, and their pore cupola organs are distinctly less attractive to ants than in related and steadily myrmecophilous species like *P. coridon* (Fiedler 1991b). Thus, *P. icarus* larvae need to invest less energy in their myrmecophilous secretions than, for example, some obligatorily myrmecophilous species (e.g., Fiedler and Maschwitz 1989b). In the field, the larvae may also receive some protection against predation or parasitism, although evidence for this is lacking.

In short, comparing our results with available data on other, and more strongly, myrmecophilous lycaenids, ant-association in *P. icarus* yields mostly benefits to males and only limited costs to females. Overall, a rather low level of myrmecophily may be advantageous in many cases. In such systems the costs of maintaining myrmecophily are comparatively low, but offer the opportunistic utilization of its related advantages whenever available ("conditional mutualism": Cushman and Addicott 1991). This could well explain why numerous lycaenid caterpillars have retained their myrmecophilous organs although their associations with ants are rather loose, and available evidence suggests that the majority of myrmecophilous lycaenid species maintain facultative ant associations (Fiedler 1991b). Total reductions of

myrmecophily ("secondary myrmecoxeny") mainly occur under peculiar ecological conditions (e.g. in arctic or alpine habitats, with endophytic caterpillars, or with food specialists on unusual and possibly less favorable hostplants: Fiedler 1991b; in continuously brooded species with high intrinsic growth rates: Robbins in press). In this scenario, the maintenance of myrmecophily appears to be the conservative and evolutionarily more stable strategy among the Lycaeninae, which is selected against only if the costs of ant association become distinctly disadvantageous.

In the North American *Glaucopsyche lygdamus* with its close, but unspecific ant association, pupal weights after hibernation did not differ between ant-tended and non-tended individuals (Pierce and Eastal 1986), suggesting that in this species also there are no severe developmental costs. Together with our results, the cases listed above support the view that the interactions of ants and lycaenid caterpillars cover a continuous wide range of cost-benefit relationships. Besides obligatory associations with high larval and pupal investments (*Jalmenus evagoras*), there are more or less close and facultative interactions with variable degrees of costs and benefits. The well-documented *Jalmenus/Iridomyrmex* system is clearly not "typical" of the Lycaenidae as a whole, and high developmental costs are not necessarily universal among the myrmecophilous lycaenids. Generalizations should thus be made with caution, even more so since only a minute fraction of the roughly 4500 described lycaenid species, probably including more than 3000 myrmecophilous ones, have so far been studied.

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