

Does ant-attendance influence development in 5 European Lycaenidae butterfly species? (Lepidoptera)

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Summary

Caterpillars and pupae of 3 myrmecophilous (*Aricia agestis*, *Polyommatus icarus*, *P. bellargus*) and 2 myrmecoxenous lycaenid butterflies (*Lycaena phlaeas*, *L. tityrus*) were reared in the laboratory together with, or without, 2 species of tending *Lasius* ants (*L. flavus*, *L. niger*). Duration of development, mass gain, growth rates, prepupal and adult weights, and the ratio of mass gain per frass production were studied. There was no evidence for significant developmental costs associated with myrmecophily. Rather, we found some marginally beneficial effects of ant-attendance. Males of *P. icarus* and *L. phlaeas* grew larger in the presence of ants. Mass gain per unit frass was slightly higher with ants in *A. agestis* (both sexes), *P. icarus* and *L. tityrus* (males only). We found no consistent differences between the effects of the 2 ant species, nor between rearing treatments involving 2 or 5 *L. flavus* workers, respectively. Sexual and interspecific differences were documented in most of the parameters. These results show that certain myrmecoxenous and facultatively myrmecophilous lycaenid butterflies are able to compensate for their energetic costs associated with myrmecophily. The evolutionary consequences of such low-cost mutualisms are discussed.

Zusammenfassung

Raupen und Puppen von 3 fakultativ myrmekophilen (*Aricia agestis*, *Polyommatus icarus* und *P. bellargus*) sowie 2 myrmekoxenen Bläulingsarten (*Lycaena phlaeas*, *L. tityrus*) wurden in Gegenwart von Ameisen (*Lasius flavus* bzw. *L. niger*) aufgezogen. Entwicklungsdauern, Wachstumsraten, Gewichte und Massenzunahme pro Kotproduktion wurden protokolliert. In keinem Fall ergab sich eine signifikante Beeinträchtigung dieser Parameter durch den Besuch von Ameisen und damit verbundene Sekretabgaben. Schwache positive

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Effekte konnten vereinzelt beobachtet werden (Gewicht der Männchen von *P. icarus* und *L. phlaeas* in Gegenwart von Ameisen größer, Massenzunahme pro Kotproduktion größer bei *A. agestis*, *P. icarus* und *L. tityrus*). Geschlechts- und Artunterschiede in den Entwicklungsparametern traten in den meisten Fällen auf. Die Ergebnisse zeigen, daß die untersuchten Bläulings-Ameisen-Interaktionen für die Schmetterlinge mit geringen, voll kompensierbaren Kosten verbunden sind. Die evolutive Bedeutung solcher Mutualismen mit niedriger Investition wird diskutiert.

Résumé

Chenilles et chrysalides de 3 Lycénides myrmécophiles (*Aricia agestis*, *Polyommatus icarus* et *P. bellargus*) et de 2 Lycénides myrmécoxènes (*Lycaena phlaeas* et *L. tityrus*) ont été élevées en laboratoire avec et sans 2 espèces de fourmis (*Lasius flavus* et *L. niger*). Les auteurs ont étudié la durée du développement, l'augmentation de taille, le taux de croissance, le poids des chenilles adultes et avant la chrysalidation, ainsi que l'augmentation de taille par rapport à la production d'excréments. Dans aucun cas, ils n'ont constaté une modification significative de ces paramètres due à la visite des fourmis. Dans quelques cas, ils ont observé de faibles effets positifs de la myrmécophilie. Le poids des mâles de *P. icarus* et *L. phlaeas* augmenta en présence des fourmis ; l'augmentation de taille par rapport à la production d'excréments fut plus marquée en présence des fourmis chez *A. agestis* (dans les deux sexes), *P. icarus* et *L. tityrus* (mâles seulement). Les auteurs n'ont pas trouvé de différences constantes entre les effets des deux espèces de fourmis, ni entre les élevages impliquant 2 ou 5 *L. flavus* (ouvrières). Des différences apparurent dans la plupart des paramètres du développement selon le sexe et l'espèce. Ces résultats montrent que les interactions Lycènes-Fourmis étudiées entraînent de faibles «coûts énergétiques», entièrement compensables. Les auteurs discutent de la signification évolutive de tels mutualismes «à faible coût».

Introduction

Many species of the butterfly family Lycaenidae live in association with ants throughout part of their larval and/or pupal stage (COTTRELL, 1984 ; PIERCE, 1987 ; FIEDLER, 1991). Ant-associations among lycaenids range from loose and unspecific, facultative interactions to obligatory and species-specific cases of mutualism or, rarely, parasitism. Typically, while feeding on their hostplants, the caterpillars attract ants with the help of chemical stimuli. This ant guard may provide protection against parasitoids or predators (PIERCE & EASTEAL, 1986 ; PIERCE *et al.*, 1987 ; but see PETERSON, 1993).

Interactions between lycaenid immatures and ants are mainly mediated by secretions from specialized exocrine epidermal glands (MALICKY,

1969; COTTRELL, 1984), although vibratory communication may be important in certain cases (DEVRIES, 1990). Three types of myrmecophilous organs are known to play major roles. The dorsal nectar organ on the 7th abdominal segment, only present in larvae, secretes droplets of a clear liquid that contain carbohydrates and amino acids (MASCHWITZ *et al.*, 1975; PIERCE, 1983) upon tactile stimulation (TAUTZ & FIEDLER, 1992). So-called pore cupola organs, minute hair-derived glands distributed over the larval or pupal integument, appear to secrete amino acids or, in certain species, mimics of ant-pheromones (PIERCE, 1983). And the tentacle organs on the 8th abdominal segment of various lycaenid caterpillar species emit volatile compounds that cause an alerted behaviour in attendant ants (FIEDLER & MASCHWITZ, 1988; BALLMER & PRATT, 1992). All these secretions are produced at some energetic cost by the herbivorous caterpillars. In addition, the innervation and musculature of myrmecophilous organs and vibratory organs also cause metabolic costs.

Previous studies on two lycaenid-ant systems demonstrated that ant-attendance may have a negative impact on larval and pupal development. In the obligatorily myrmecophilous *Jalmenus evagoras* (DONOVAN, 1805) from Australia, ant-tended individuals develop faster than untended sisters, but attain lower weights (PIERCE *et al.*, 1987). Larvae of *J. evagoras* are unable to compensate for nutrient loss to ants (BAYLIS & PIERCE, 1992). As a consequence, myrmecophily is associated with significant fitness costs, since male mating success and female fecundity are strongly dependent on adult weight (ELGAR & PIERCE, 1988; HILL & PIERCE, 1989). In the Neotropical *Arawacus lincoides* (Draudt, [1919]), ROBBINS (1991) observed a slight retardation of larval development in response to ant-association, but weight was unaffected.

Recently, however, beneficial effects of ant-attendance on larval development have been detected in three additional species. FIEDLER & HÖLDOBLER (1992) found that ant-tended males of the Palearctic *Polyommatus icarus* (Rottemburg, 1775) reach higher larval and pupal weights than untended controls. In the Nearctic *Hemiargus isola* (Reakirt, [1867]), tending by the ant *Formica perpilosa* enhanced caterpillar growth and thus adult weight, whereas two other ant species did not affect butterfly weight (WAGNER, 1993). These two butterfly species are facultative myrmecophiles, whose larvae associate with a variety of ant taxa and are not dependent on ant-association for survival. Overall, facultative myrmecophiles account for a larger proportion of the species diversity of the Lycaenidae than obligatory myrmecophiles (FIEDLER, 1991). Most recently, CUSHMAN *et al.* (1994) observed bene-

ficial developmental effects in another Australian obligatory myrmecophile, *Paralucia aurifera* (Blanchard, 1848). Hence, the prominent developmental costs of myrmecophily as found in *J. evagoras* might be atypical for the species majority. Therefore, a better understanding of the evolutionary and ecological significance of developmental costs or benefits arising from myrmecophily among Lycaenidae butterflies requires experimental work on a larger set of species from various taxonomic groups and representing all major types of myrmecophily.

We here present the results of laboratory experiments with 5 European Lycaenidae species. Three of these possess all three types of myrmecophilous organs and are facultative myrmecophiles, but show different degrees of myrmecophily. While mature larvae of *Polyommatus bellargus* (Rottemburg, 1775) and *Arícia agestis* ([Denis & Schiffermüller], 1775) are rarely found without tending ants in nature, caterpillars of *Polyommatus icarus* are much less attractive to ants (e.g. THOMAS & LEWINGTON, 1991). *P. icarus* was included to repeat the experiments of FIEDLER & HÖLLDOBLER (1992) under a modified rearing regime. We also studied two myrmecoxenous species: *Lycaena phlaeas* (Linnaeus, 1761) and *L. tityrus* (Poda, 1761). Larvae of these species neither possess a dorsal nectar organ nor tentacle organs, but they do have pore cupola organs. In laboratory experiments, weak and unstable ant-associations of these species can be induced and ants then harvest the PCO secretions (FIEDLER, 1991). Neither *L. phlaeas* nor *L. tityrus* larvae have hitherto been observed in association with ants in the field.

Our aim was to investigate whether or not artificial ant-association involving two ant species and two different numbers of ants per individual lycaenid has any detectable effects on larval or pupal development. Furthermore, we wanted to know whether developmental effects differ between lycaenid species according to their degree of myrmecophily. One might expect more distinct costs in caterpillars that are highly attractive to ants (*P. bellargus*, *A. agestis*), whereas in myrmecoxenous species developmental costs should be absent or minimal. On the other extreme, secretion rates of obligatorily myrmecophilous caterpillars can be amazingly high (FIEDLER & MASCHWITZ, 1989; Fiedler, unpublished), corresponding to the pronounced developmental costs observed in species like the Australian *Jalmenus evagoras* (BAYLIS & PIERCE, 1992). Finally, the developmental constraints on phytopredacious lycaenid larvae parasitizing inside ant colonies (alike the Palearctic *Maculinea* spp.) are entirely different (e.g. THOMAS *et al.*, 1993, and references therein). Hence, a comparative survey across a larger number of species representing various stages of myrmecophily appears rewarding.

Material and methods

Butterfly rearing

Caterpillars were reared from eggs laid by field-caught (*Aricia agestis*, *Polyommatus bellargus*, *P. icarus*, *Lycaena phlaeas*, *L. tityrus*) or laboratory-bred females (*A. agestis*, *P. icarus*). Livestock originated from northern Bavarian populations except in *P. bellargus*, where part of the experiments was conducted with individuals from southern France. Butterflies were kept in a greenhouse for oviposition or mating. Rearing procedures largely followed those described by SCHURIAN (1989). Eggs were collected every second day and transferred into a climatic chamber (25°C, 16:8 h L:D), where the whole development to adult eclosion took place. Groups of first instar larvae were placed in translucent plastic containers (125 ml) lined with moist filter paper. They were fed with cut foliage or inflorescences of appropriate host-plants: *Geranium molle* L. (Geraniaceae) leaves (*A. agestis*); *Coronilla varia* L. (Fabaceae) leaves (*P. bellargus*); *Medicago sativa* L. (Fabaceae) inflorescences (*P. icarus*); *Rumex acetosa* L. (Polygonaceae) leaves (*Lycaena phlaeas*, *L. tityrus*). Food was exchanged daily. Special care was taken to provide food of approximately equal quality ad libitum throughout the season, since food quality may affect larval myrmecophily (FIEDLER, 1990; BAYLIS & PIERCE, 1991).

Ants

Two ant species were used. *Lasius niger* (Linnaeus, 1758) is a common species of open grasslands and is well known to tend a number of lycaenid species in the field (FIEDLER, 1991). *L. niger* ants are omnivorous; they feed on insect prey and collect honeydew or similar energy-rich fluids. *Lasius flavus* (Fabricius, 1781) is also very common and lives largely subterranean in European grasslands. Its diet consists almost entirely of honeydew produced by root aphids. Because of their subterranean life, *L. flavus* ants rarely tend lycaenid larvae in nature, but they readily show trophobiotic interactions with lycaenid immatures in the laboratory (FIEDLER, 1991). Ant colonies were kept in the laboratory (at 22-26°C) in earth nests (*L. flavus*), or in artificial nest chambers the bottom of which consisted of plaster of Paris (*L. niger*). Ants were fed with honey-water and dead insects (mostly cockroaches) as needed.

Experiments

Experiments started at the beginning of the third larval instar, when the myrmecophilous glands of *P. icarus*, *P. bellargus* and *A. agestis*

become functional. Experimental caterpillars were reared singly in translucent plastic vials (125 ml) equipped as above and were randomly subjected to one of the 4 following treatments : kept with 5 *L. flavus* workers ; with 2 *L. flavus* workers ; with 2 *L. niger* workers ; and controls reared without ants. Food and filter paper were exchanged daily, and the entire larval frass was collected. Ants that had died during the experiment were replaced by nestmates to ensure a constant number of tending ants throughout. The procedure continued during the pupal stage. Daily inspections of every individual larva and pupa confirmed that all immatures of the 3 myrmecophilous species were constantly tended by their ant guard. In the 2 *Lycaena* species, ant-associations were likewise regularly observed, although occasionally larvae were seen without tending ants for short periods of time. Each experiment lasted until the adult butterfly eclosed from the pupa. All individuals that died prior to eclosion were discarded from the analyses. Mortality rates did not differ between the ant treatments within each species (SAAM, 1993). In total, 358 butterflies were reared to maturity (see SAAM, 1993 for further details).

Every individual was weighed 5 times : at the beginning of the experiment (freshly moulted L3 : initial larval weight) ; as immobile non-feeding prepupa within a few hours prior to pupation (prepupal weight) ; as freshly moulted pupa (initial pupal weight) ; as fully pigmented pupa within 6 h before eclosion ; and as freshly eclosed adult after emission of the meconium (adult weight). The whole frass production over the third and fourth larval instar was collected, dried in an oven at 65°C to constant weight, and then weighed. All weights were recorded to the nearest 0.1 mg using an electronic Sartorius BA 61 balance. In addition, the durations of the third plus fourth larval instars and of the pupal stage were recorded (in days).

From these data the following additional parameters were calculated :

PERCENT PUPAL WEIGHT LOSS : $(\text{Initial pupal weight} - \text{final pupal weight}) \times 100 / (\text{initial pupal weight})$. Pupal weight losses always occur during development, but could be enhanced by the delivery of pupal secretions (e.g. from pore cupola organs) to ants.

RELATIVE GROWTH RATE : $\text{RGR} = (\text{mass gained in the third plus fourth larval instar}) / (\text{prepupal weight} \times \text{larval duration})$.

The ratio : $(\text{larval mass gain}) / (\text{total frass production})$. This is a rough estimate for the efficiency of the conversion of ingested food into biomass. Assuming that the digestibility of food is not affected by the

presence of ants (see BAYLIS & PIERCE, 1992), frass production is proportional to food consumption, if food quality is kept constant.

The data were analysed statistically using ANOVA (with sex and treatment as factors) for multiple comparisons, and Mann-Whitney U-tests for comparisons between pairs of samples where normality or homogeneity of variances were not met (SACHS, 1992). Percent data were arcsine-transformed prior to analysis. All P values given refer to 2-tailed tests.

Results

Duration of larval and pupal development

The duration of the third plus fourth instar (Table 1) was largely unaffected by the presence of ants in *A. agestis* (mean values per experimental series 6-9 d), *P. icarus* (10-12 d), *P. bellargus* (16-23 d), *L. phlaeas* (8-10 d) and *L. tityrus* (11-15 d). Sex differences in the duration of larval development occurred in all 5 species and in almost all treatments. Females generally took 1-2 d longer than males until pupation, but this difference was less distinct in experiments with *P. icarus* and *L. phlaeas*.

The duration of the pupal stage was likewise not influenced by ant-association in all 5 lycaenid species tested. Sex differences in pupal duration were minimal (males faster in *L. tityrus* and *P. bellargus*). The pupal stage of *A. agestis*, *L. phlaeas* and *L. tityrus* took 7-8 d, that of *P. icarus* 9-10 d, and in *P. bellargus* pupal development lasted 11-13 d under the rearing conditions.

Prepupal weights (Table 2)

Caterpillar mass at the end of the larval stage was independent of ant-association in *A. agestis* (means 71-82 mg), *P. bellargus* (means 107-126 mg) and *L. tityrus* (118-127 mg). *P. icarus* males reared in the presence of ants (94.55 ± 1.33 mg) were consistently heavier than control males (89.46 ± 5.44 mg), although the difference was not significant. However, ant-association fostered a sex difference in *P. icarus*. Males reared in the presence of ants were significantly heavier than females ($U_{23;31} = 195$; $Z = 2.825$; $P < 0.01$), whereas control males and females reached equal prepupal weights ($U_{7;13} = 45$; $P > 0.5$). A similar pattern occurred in *L. phlaeas*. Male prepupae reared in association with ants (89.6 ± 3.05 mg) were significantly heavier than controls (73.8 ± 2.34 mg; $U_{10;24} = 38$; $Z = 3.099$; $P < 0.01$),

Table 1

Duration of larval development (third plus fourth instar, in days) of five European Lycaenidae species when reared in the presence or absence of *Lasius* ants. Given are means \pm standard errors (sample sizes in brackets). F values are from two-way ANOVA. + $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns $P > 0.10$.

Species	5 <i>Lasius flavus</i>	2 <i>Lasius flavus</i>	2 <i>Lasius niger</i>	Without ants	Effect	Ant. treatments combined	Effect
<i>Aricia agestis</i>							
Females	8.07 \pm 0.36 (15)	8.29 \pm 0.33 (17)	9.14 \pm 0.34 (7)	8.53 \pm 0.30 (17)	treatment : F = 2.14 ns	8.36 \pm 0.21 (39)	ants : F = 0.74 ns
Males	6.86 \pm 0.40 (7)	7.56 \pm 0.29 (9)	7.71 \pm 0.36 (7)	7.75 \pm 0.45 (8)	sex : F = 13.91***	7.39 \pm 0.21 (23)	sex : F = 8.07**
<i>Polyommatus icarus</i>							
Females	11.50 \pm 0.42 (8)	11.75 \pm 0.31 (8)	11.50 \pm 0.67 (6)	11.62 \pm 0.45 (13)	treatment : F = 0.37 ns	11.59 \pm 0.25 (22)	ants : F = 0.94 ns
Males	11.00 \pm 0.24 (11)	10.63 \pm 0.42 (8)	11.17 \pm 0.32 (12)	11.57 \pm 0.37 (7)	sex : F = 2.92+	10.97 \pm 0.18 (31)	sex : F = 1.06 ns
<i>Polyommatus bellargus</i>							
Females	21.17 \pm 1.47 (6)	20.50 \pm 1.16 (8)	19.14 \pm 0.70 (7)	22.50 \pm 1.21 (8)	treatment : F = 3.91*	20.24 \pm 0.65 (21)	ants : F = 2.68 ns
Males	19.00 \pm 0.93 (8)	16.50 \pm 1.33 (4)	20.00 \pm 1.16 (4)	19.57 \pm 1.67 (7)	sex : F = 4.06*	18.63 \pm 0.68 (16)	sex : F = 5.38*
<i>Lycaena phlaeas</i>							
Females	9.57 \pm 0.53 (7)	9.22 \pm 0.22 (9)	9.27 \pm 0.24 (11)	8.40 \pm 0.40 (5)	treatment : F = 1.30 ns	9.33 \pm 0.18 (27)	ants : F = 2.03 ns
Males	8.72 \pm 0.27 (11)	8.33 \pm 0.31 (7)	8.83 \pm 0.17 (6)	8.80 \pm 0.29 (10)	sex : F = 4.11*	8.63 \pm 0.16 (24)	sex : F = 0.34 ns
<i>Lycaena tityrus</i>							
Females	12.57 \pm 0.84 (7)	14.67 \pm 0.76 (6)	13.89 \pm 0.77 (9)	13.43 \pm 0.68 (7)	treatment : F = 0.71 ns	13.68 \pm 0.48 (22)	ants : F = 0.54 ns
Males	11.92 \pm 0.57 (13)	11.43 \pm 0.68 (7)	12.00 \pm 0.71 (8)	11.27 \pm 0.38 (11)	sex : F = 16.83***	11.82 \pm 0.36 (28)	sex : F = 13.61***

Table 2
Final larval weights (in prepupal stage, mg wet weight) of five European Lycaenidae species when reared in the presence or absence of *Lasius* ants. Given are means \pm standard errors (sample sizes in brackets). F values are from two-way ANOVA. * $P < 0.05$; ** $P < 0.01$; ns $P > 0.10$.

Species	5 <i>Lasius flavus</i>	2 <i>Lasius flavus</i>	2 <i>Lasius niger</i>	Without ants	Effect	Ant treatments combined	Effect
<i>Aricia agestis</i> Females Males	76.02 \pm 2.04 (17) 76.56 \pm 2.49 (8)	80.10 \pm 2.19 (18) 71.42 \pm 2.03 (10)	81.81 \pm 5.40 (7) 71.51 \pm 3.22 (7)	77.47 \pm 1.75 (19) 73.98 \pm 2.71 (9)	treatment : F = 0.05 ns sex : F = 7.76**	78.74 \pm 1.59 (42) 73.09 \pm 1.47 (25)	ants : F = 0.01 ns sex : F = 4.63*
<i>Polyommatus icarus</i> Females Males	89.63 \pm 2.51 (8) 92.63 \pm 2.23 (11)	88.13 \pm 2.38 (8) 92.40 \pm 2.05 (8)	86.21 \pm 3.70 (7) 97.73 \pm 2.25 (12)	89.19 \pm 2.73 (13) 89.46 \pm 5.44 (7)	treatment : F = 0.29 ns sex : F = 5.16*	88.07 \pm 1.60 (23) 94.55 \pm 1.33 (31)	ants : F = 0.70 ns sex : F = 2.02 ns
<i>Polyommatus bellargus</i> Females Males	106.52 \pm 6.55 (6) 117.83 \pm 1.88 (8)	109.63 \pm 4.24 (8) 115.48 \pm 8.43 (4)	112.10 \pm 4.46 (7) 125.23 \pm 5.18 (4)	113.69 \pm 5.76 (8) 126.07 \pm 5.24 (7)	treatment : F = 1.15 ns sex : F = 8.08**	109.56 \pm 2.77 (21) 119.12 \pm 2.58 (16)	ants : F = 1.99 ns sex : F = 7.80**
<i>Lycaena phlaeas</i> Females Males	89.67 \pm 4.84 (7) 88.24 \pm 5.50 (11)	98.70 \pm 6.37 (9) 85.50 \pm 5.56 (7)	90.64 \pm 4.49 (11) 93.50 \pm 2.87 (6)	83.42 \pm 8.39 (6) 73.80 \pm 2.34 (10)	treatment : F = 3.08* sex : F = 1.45 ns	93.07 \pm 3.06 (27) 89.60 \pm 3.05 (24)	ants : F = 8.28** sex : F = 2.19 ns
<i>Lycaena tityrus</i> Females Males	118.11 \pm 6.77 (7) 119.23 \pm 3.61 (13)	127.00 \pm 4.98 (6) 119.37 \pm 4.76 (7)	126.01 \pm 5.77 (9) 125.13 \pm 3.86 (8)	121.27 \pm 7.59 (7) 121.56 \pm 5.01 (11)	treatment : F = 0.58 ns sex : F = 0.22 ns	123.77 \pm 3.42 (22) 120.95 \pm 2.30 (28)	ants : F = 0.05 ns sex : F = 0.09 ns

whereas females showed no effect (mean weights 83.42 ± 8.39 mg and 93.07 ± 3.06 mg ; $U_{6;27} = 51$; $Z = 1.40$; $P = 0.17$).

A general sex difference in prepupal weights emerged only in 2 species. *A. agestis* males were smaller than females, in *P. bellargus* males were larger. In *P. icarus* and *L. phlaeas*, the sex difference was only apparent in ant-tended individuals (males larger than females, see above). Females and males of *L. tityrus* reached similar prepupal weights. Significant statistical ant-sex interactions were not observed.

Pupal weight loss

In all 5 species, ant-association had no detectable influence on pupal weight loss. Mean weight losses accounted for 15-20% in *A. agestis*, *P. icarus* and *L. phlaeas*, but were slightly higher in *L. tityrus* ($> 20\%$ in females) and highest in *P. bellargus* (average values per series 23-28%). Sex differences in pupal weight loss were distinct only in *L. tityrus* (female pupae lost more weight [22-24% on average] than males [average loss 17-19%]). Otherwise, there were neither sex differences nor significant ant-sex interactions.

Adult weights (Table 3)

Adult weights were not affected by ant-association in *A. agestis*, *P. bellargus* and *L. tityrus*. In *P. icarus*, ant-tended males (35.07 ± 0.76 mg) were ca. 10% heavier than untended controls (31.27 ± 1.21 mg ; $U_{7;31} = 50$; $Z = 2.20$; $P < 0.02$), whereas females showed no effect (ant-sex interaction : $F_{1;67} = 3.92$; $P < 0.05$). A similar effect was observed in *L. phlaeas* : ant-tended individuals (especially males : 31.41 ± 1.70 mg) eclosed from the pupae at higher weights than untended controls (23.65 ± 0.85 mg). As a consequence, there was no significant sex difference in adult weights of ant-tended *P. icarus* and *L. phlaeas*, whereas untended controls of both species showed a distinct size dimorphism (females heavier than males). In *A. agestis* there was a significant sex difference independent of ant-association, females being heavier than males. No significant size dimorphism occurred in *P. bellargus* and *L. tityrus*.

Growth rates (Table 4)

In all 5 species tested, males tended to grow faster than females. This difference was only weakly developed in *P. icarus* and *L. phlaeas*, but was pronounced in the remaining 3 species. Only in *A. agestis* was there a weak trend that caterpillars in association with 5 *Lasius flavus* ants grew slightly faster than all others. In all, ant-association had no

Table 3

Adult weights (mg wet weight) of five European Lycaenidae species when reared in the presence or absence of *Lasius* ants.
Given are means \pm standard errors (sample sizes in brackets).

F values are from two-way ANOVA, + $P < 0.1$; * $P < 0.05$; *** $P < 0.001$; ns $P > 0.10$.

Species	5 <i>Lasius flavus</i>	2 <i>Lasius flavus</i>	2 <i>Lasius niger</i>	Without ants	Effect	Ant treatments combined	Effect
<i>Aricia agestis</i> Females Males	30.72 \pm 1.22 (17) 26.13 \pm 0.97 (8)	30.66 \pm 1.29 (18) 25.21 \pm 0.69 (10)	35.96 \pm 3.38 (7) 24.01 \pm 1.05 (7)	31.24 \pm 1.28 (19) 25.51 \pm 1.14 (9)	treatment : F = 0.65 ns sex : F = 38.76***	31.57 \pm 0.95 (42) 25.17 \pm 0.51 (25)	ants : F = 0.01 ns sex : F = 29.34***
<i>Polyommatus icarus</i> Females Males	36.54 \pm 1.28 (7) 35.41 \pm 1.40 (11)	35.26 \pm 0.94 (8) 35.01 \pm 1.13 (8)	33.34 \pm 0.89 (5) 34.80 \pm 1.38 (12)	35.94 \pm 1.57 (13) 31.27 \pm 1.21 (7)	treatment : F = 1.04 ns sex : F = 1.20 ns	35.23 \pm 0.65 (20) 35.07 \pm 0.76 (31)	ants : F = 1.84 ns sex : F = 4.49*
<i>Polyommatus bellargus</i> Females Males	35.42 \pm 4.47 (6) 42.04 \pm 3.51 (8)	41.48 \pm 3.22 (8) 38.23 \pm 3.28 (4)	38.00 \pm 2.30 (7) 43.22 \pm 4.32 (4)	41.60 \pm 2.93 (8) 43.20 \pm 3.38 (7)	treatment : F = 0.37 ns sex : F = 1.01 ns	38.59 \pm 1.91 (21) 41.38 \pm 2.14 (16)	ants : F = 0.83 ns sex : F = 0.68 ns
<i>Lycaena phlaeas</i> Females Males	31.09 \pm 2.67 (7) 31.63 \pm 3.23 (11)	37.30 \pm 4.22 (8) 31.08 \pm 2.44 (6)	32.23 \pm 2.32 (11) 31.35 \pm 2.14 (6)	30.27 \pm 3.00 (6) 23.65 \pm 0.85 (10)	treatment : F = 2.15 ns sex : F = 2.57 ns	33.48 \pm 1.77 (26) 31.41 \pm 1.70 (23)	ants : F = 5.49* sex : F = 3.43+
<i>Lycaena tityrus</i> Females Males	40.52 \pm 2.18 (7) 39.89 \pm 2.64 (13)	46.42 \pm 2.60 (6) 41.13 \pm 2.45 (7)	47.56 \pm 3.06 (9) 44.37 \pm 3.52 (7)	44.06 \pm 3.50 (7) 42.18 \pm 2.34 (11)	treatment : F = 1.25 ns sex : F = 1.67 ns	45.22 \pm 1.72 (21) 41.37 \pm 1.67 (27)	ants : F = 0.01 ns sex : F = 1.48 ns

Table 4

Relative growth rates (in mg/mg * d) of five European Lycaenidae species when reared in the presence or absence of *Lasius* ants.
Given are means \pm standard errors (sample sizes in brackets).

F values are from two-way ANOVA. + $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns $P > 0.10$.

Species	5 <i>Lasius flavus</i>	2 <i>Lasius flavus</i>	2 <i>Lasius niger</i>	Without ants	Effect	Ant treatments combined	Effect
<i>Aricia agestis</i> Females Males	0.114 \pm 0.004 (17) 0.130 \pm 0.005 (8)	0.111 \pm 0.003 (18) 0.119 \pm 0.005 (10)	0.104 \pm 0.003 (7) 0.118 \pm 0.004 (7)	0.108 \pm 0.003 (19) 0.117 \pm 0.005 (9)	treatment : F = 2.58+ sex : F = 14.77***	0.111 \pm 0.002 (42) 0.122 \pm 0.003 (25)	ants : F = 1.46 ns sex : F = 9.56**
<i>Polyommatus icarus</i> Females Males	0.085 \pm 0.003 (8) 0.089 \pm 0.002 (11)	0.083 \pm 0.002 (8) 0.091 \pm 0.003 (8)	0.086 \pm 0.004 (7) 0.088 \pm 0.003 (12)	0.084 \pm 0.003 (13) 0.084 \pm 0.003 (7)	treatment : F = 0.59 ns sex : F = 3.30+	0.085 \pm 0.002 (23) 0.089 \pm 0.001 (31)	ants : F = 1.72 ns sex : F = 1.20 ns
<i>Polyommatus bellargus</i> Females Males	0.046 \pm 0.003 (6) 0.051 \pm 0.002 (8)	0.047 \pm 0.002 (8) 0.059 \pm 0.005 (4)	0.051 \pm 0.002 (7) 0.048 \pm 0.003 (4)	0.043 \pm 0.002 (8) 0.050 \pm 0.004 (7)	treatment : F = 1.81 ns sex : F = 6.30*	0.048 \pm 0.001 (21) 0.052 \pm 0.002 (16)	ants : F = 2.30 ns sex : F = 5.78*
<i>Lycaena phlaeas</i> Females Males	0.102 \pm 0.005 (7) 0.111 \pm 0.004 (11)	0.105 \pm 0.003 (9) 0.116 \pm 0.005 (7)	0.105 \pm 0.003 (11) 0.110 \pm 0.002 (6)	0.106 \pm 0.011 (6) 0.110 \pm 0.003 (10)	treatment : F = 1.07 ns sex : F = 3.77+	0.104 \pm 0.002 (27) 0.113 \pm 0.002 (24)	ants : F = 0.04 ns sex : F = 2.92+
<i>Lycaena tityrus</i> Females Males	0.079 \pm 0.005 (7) 0.084 \pm 0.004 (13)	0.068 \pm 0.004 (6) 0.086 \pm 0.005 (7)	0.072 \pm 0.004 (9) 0.083 \pm 0.004 (8)	0.074 \pm 0.004 (7) 0.087 \pm 0.002 (11)	treatment : F = 0.58 ns sex : F = 17.15***	0.073 \pm 0.003 (22) 0.084 \pm 0.002 (28)	ants : F = 0.27 ns sex : F = 14.21***

Table 5

Ratio of larval mass gain and frass production (mg wet weight/mg dry weight) of five European Lycaenidae species when reared in the presence or absence of *Lasius* ants. Given are means \pm standard errors (sample sizes in brackets). F values are from two-way ANOVA. + $P < 0.1$; * $P < 0.05$; ns $P > 0.10$.

Species	5 <i>Lasius flavus</i>	2 <i>Lasius flavus</i>	2 <i>Lasius niger</i>	Without ants	Effect	Ant treatments combined	Effect
<i>Aricia agestis</i> Females Males	1.51 \pm 0.10 (17) 1.49 \pm 0.08 (8)	1.46 \pm 0.08 (18) 1.41 \pm 0.08 (10)	1.69 \pm 0.11 (7) 1.46 \pm 0.08 (7)	1.34 \pm 0.06 (19) 1.34 \pm 0.11 (9)	treatment : F = 2.07 ns sex : F = 1.10 ns	1.52 \pm 0.06 (42) 1.45 \pm 0.05 (25)	ants : F = 3.69+ sex : F = 0.22 ns
<i>Polyommatus icarus</i> Females Males	1.70 \pm 0.07 (8) 2.04 \pm 0.15 (11)	1.78 \pm 0.22 (8) 1.91 \pm 0.18 (8)	1.82 \pm 0.25 (7) 2.15 \pm 0.12 (12)	1.81 \pm 0.09 (13) 1.89 \pm 0.06 (7)	treatment : F = 0.38 ns sex : F = 4.21*	1.76 \pm 0.10 (23) 2.05 \pm 0.08 (31)	ants : F = 0.23 ns sex : F = 2.34 ns
<i>Polyommatus bellargus</i> Females Males	1.88 \pm 0.14 (6) 1.90 \pm 0.12 (8)	1.75 \pm 0.08 (8) 2.10 \pm 0.19 (4)	1.45 \pm 0.07 (7) 1.71 \pm 0.21 (4)	1.94 \pm 0.10 (8) 2.06 \pm 0.16 (7)	treatment : F = 3.91* sex : F = 4.06*	1.68 \pm 0.07 (21) 1.90 \pm 0.09 (16)	ants : F = 3.85+ sex : F = 2.63 ns
<i>Lycaena phlaeas</i> Females Males	3.97 \pm 0.31 (7) 3.96 \pm 0.28 (11)	3.98 \pm 0.38 (9) 4.97 \pm 0.66 (6)	4.62 \pm 0.30 (11) 3.92 \pm 0.21 (5)	3.64 \pm 0.26 (6) 4.22 \pm 0.36 (10)	treatment : F = 0.95 ns sex : F = 0.67 ns	4.23 \pm 0.19 (27) 4.22 \pm 0.24 (22)	ants : F = 0.91 ns sex : F = 0.86 ns
<i>Lycaena tityrus</i> Females Males	3.47 \pm 0.36 (7) 4.31 \pm 0.33 (13)	3.87 \pm 0.24 (6) 4.25 \pm 0.39 (7)	3.58 \pm 0.22 (9) 4.08 \pm 0.34 (8)	3.53 \pm 0.14 (7) 3.30 \pm 0.24 (11)	treatment : F = 1.51 ns sex : F = 2.77+	3.62 \pm 0.16 (22) 4.23 \pm 0.20 (28)	ants : F = 4.36* sex : F = 0.58 ns

significant influence on growth rates. Relative growth rates (daily mass gain divided by prepupal mass) were 0.10-0.13 mg/mg * d in *A. agestis* and *L. phlaeas*, 0.07-0.09 mg/mg * d in *P. icarus* and *L. tityrus*, and 0.045-0.05 mg/mg * d in *P. bellargus*.

Frass production and efficiency of food conversion (Table 5)

The ratio of larval mass gain (wet weight) and frass production (dry weight) was at most weakly affected by ant-association in all 5 species. In *P. bellargus*, this ratio was lower in the experimental series with 2 *L. niger* ants. This series was reared later in the season than all others, and the differences most likely indicate a change in hostplant quality rather than any influence of ant-tending. In *A. agestis*, *L. phlaeas* and *L. tityrus*, no consistent effects of ants were found. For *P. icarus*, ANOVA indicated no influence of ant-association on food utilization. However, ant-tended males had a significantly higher mass gain/frass ratio than ant-tended females ($U_{23;31} = 170$; $Z = 3.26$; $P < 0.002$), whereas in control experiments this sex difference did not occur ($U_{7;13} = 34$; $P > 0.2$). Overall, sex differences in this parameter were minimal, and average values for the treatments ranged from 1.34-1.52 mg/mg in *A. agestis*, 1.70-2.05 mg/mg in both *Polyommatus* species, and 3.30-4.97 mg/mg in the two *Lycaena* species.

Discussion

Differences in developmental parameters between males and females were observed in all 5 species tested. Generally males developed faster (shorter larval period, higher growth rate). This is in accordance with the protandry of all 5 species in nature.

All species examined produce 2 or more generations per year in central or southern Europe. The most rapid development was observed in *A. agestis* and *L. phlaeas*. These two species produce 3-4 generations per year in central Europe in favourable seasons. *P. icarus* was somewhat slower (2-3 generations per year), and *L. tityrus* as well as *P. bellargus* took longest to reach maturity. In the latter two species a third generation is a very rare exception north of the Alps (EBERT & RENN-WALD, 1991). Thus, our laboratory results are consistent with phenological observations made in the field.

Pupal weight losses were highest in *P. bellargus*, the species with the longest pupal stage, and were fairly similar among the remaining 4 species. Concerning the ratio of mass gain per frass production, the two myrmecoxenous *Lycaena* species far surpassed the 3 myrmecophilous members of the *Polyommatus* group. Both *Lycaena* species

feed on leaves of *Rumex* species (Polygonaceae). These leaves appear to have a lower content of undigestible material than the legume hostplants of *P. icarus* or *P. bellargus*. PIERCE (1985) has argued that myrmecophily has selected for the utilization of nutrient-rich hostplants (especially nitrogen-rich legumes and inflorescences), but obviously the 2 *Lycaena* species perform in a superior manner on the foliage of a non-legume host. According to its biomass/frass ratio, *A. agestis* utilizes the poorest hostplant material (leaves of Geraniaceae), but nevertheless the caterpillars are highly myrmecophilous. The nutritional constraints on larval myrmecophily are a rewarding field open to further investigation (BAYLIS & PIERCE, 1993).

Overall, ants had very little impact on the developmental parameters studied, and the few marginally significant ant-effects which could be detected were mostly beneficial. From facultatively myrmecophilous Lycaenidae butterflies like *Polyommatus icarus* or *Hemiargus isola* it is already known that ant-association does not necessarily pose developmental costs, but may even allow overcompensation of the investment into myrmecophily (FIEDLER & HÖLLDOBLER, 1992 ; WAGNER, 1993). Our present data fully corroborate that pattern.

Aricia agestis and *Polyommatus bellargus* are both facultative myrmecophiles whose older larvae are almost never found without tending ants (e.g. THOMAS & LEWINGTON, 1991). In these species, ant-association had very limited effects on developmental parameters, suggesting that larvae of both sexes can fully compensate for the costs of myrmecophily. In recent experiments with *A. agestis*, we could even demonstrate a beneficial effect of ant-attendance on prepupal weights (tended individuals are ca. 10% heavier, but develop more slowly : Hummel & Fiedler, unpublished). *Polyommatus icarus* is a facultative myrmecophile with a rather loose relationship to ants (THOMAS & LEWINGTON, 1991). Caterpillars of this species produce less secretion from their nectar organs than *P. coridon* and its close relatives (FIEDLER, 1991), suggesting a comparatively low energetic investment into myrmecophily. Our experimental data confirm the findings of FIEDLER & HÖLLDOBLER (1992) that ant-tended *P. icarus* males grow larger than untended controls, whereas tended females appear to fully compensate for their costs of myrmecophily.

Weak male-limited benefits also occurred in myrmecoxenous *Lycaena* species (weight in *L. phlaeas*, food conversion in *L. tityrus*). Caterpillars of both species lack a dorsal nectar organ. Accordingly, their energetic investment in interactions with ants must be low (only through the ubiquitous pore cupola organs). Ant-associations of these species are

unknown in the wild, but under laboratory conditions weak and unstable associations can be induced (FIEDLER, 1991).

As in the case of certain ant-tended aphids which show better growth in the presence of ants (BANKS & NIXON, 1958), the physiological mechanisms responsible for overcompensation in some lycaenid caterpillars remain unclear. Ant-tended caterpillars did not produce more frass than untended controls (SAAM, 1993). Therefore, total food consumption was probably equal between the groups. Rather, the efficiency of food conversion into biomass may be stimulated by tending ants. Circumstantial evidence for this hypothesis was found in *A. agestis*, *P. icarus* and *L. tityrus*, where ant-tended individuals showed enhanced conversion of food.

Alternatively, the stimulation of caterpillars could be a predominantly behavioural phenomenon (see discussion in WAGNER, 1993). Perhaps feeding behaviour is less often interrupted in ant-tended individuals, facilitating a more effective food utilization. Caterpillars of *P. icarus*, *P. coridon* and other myrmecophilous species resume locomotion and feeding more rapidly after experimental disturbance when ants are present (Fiedler, unpublished). In the Nearctic *Glaucopsyche lygdamus* (Doubleday, 1841), untended caterpillars are much more likely to drop off the hostplant (PIERCE & EASTEAL, 1986). Developmental effects of ant-attendance have not been studied in detail in this latter species, but pupal weights of tended and untended individuals did not differ (PIERCE & EASTEAL, 1986).

One could argue that, under the confined conditions of artificial ant-associations, ants do not harvest larval secretions as eagerly as they would do if they could transfer their crop content to their colony. Three lines of evidence contradict this view. Firstly, caterpillars and pupae of all 5 species tested were regularly tended by ants (and the 3 myrmecophilous species constantly so) throughout the whole experimental period. Tending levels did not decrease with time. This indicates that the ants, which had no access to alternative food sources, exerted a permanent pressure on the lycaenid immatures to deliver their secretions. Secondly, in *P. icarus* (and in the myrmecoxenes *L. phlaeas* and *L. tityrus*) the numbers of ants per larva used in our experiments were comparable to, or even higher than, the average number of tending ants observed so far in nature. Hence, at least in these species compensation or overcompensation occurred despite a relatively high level of ant-attendance.

Thirdly, the amounts of nectar secretion produced by single lycaenid larvae over the third plus fourth instar are sufficiently small to be

sampled completely by a small number of ant workers. In *P. icarus* and *A. agestis*, for example, individual lifetime nectar secretion volumes amount to 10 μ l or less, equivalent to approximately 1.5 mg carbohydrates at most (Fiedler, Burghardt & Hummel, unpublished). However, we cannot rule out the possibility that in future experiments (e.g. with higher tending levels or involving other ant species) deviating results could be obtained. The actual outcome of potentially mutualistic interspecific interactions can be strongly shaped by environmental conditions such as hostplant quality or density of interacting species (CUSHMAN & WHITHAM, 1991 ; BRETON & ADDICOTT, 1992).

There is steadily increasing evidence that compensation or even over-compensation of the energetic costs resulting from ant-association is not uncommon among facultatively myrmecophilous lycaenid butterflies. This finding could explain why facultative, and sometimes weak, interactions with ants are so common and taxonomically widespread across the diversity of Lycaenidae butterflies (FIEDLER, 1991). If myrmecophily were generally a high-cost strategy under severe selective regimes, one would have to expect strong disruptive selection favouring either close and obligatory myrmecophily with high costs, but high rewards for the lycaenids, or favouring the reduction of myrmecophily. In contrast to this expectation, facultative ant-associations appear to be more common in lycaenid butterflies than cases of obligatory myrmecophily (PIERCE, 1987 ; FIEDLER, 1991). Many examples of facultative interactions with ants are probably best described as low-cost mutualisms, where the lifetime energetic investment of individual caterpillars accounts for a few μ l of secretions. It is then not surprising that myrmecophily is an evolutionarily rather stable component in the life-history of so many Lycaenidae species.

A broad continuum of cost-benefit relationships in terms of myrmecophily does exist across the diversity of Lycaenidae butterflies. This is reflected by the variety of developmental effects these ant-association can have in various lycaenid species, ranging from severe costs to substantial benefits. In general, the developmental costs for the larvae appear to parallel the degree of obligateness of the ant-lycaenid associations : the more dependent the larvae are on ants, the higher the costs the ants can in turn impose. Further comparative studies on species representing various taxonomic groups and different types of myrmecophily will strengthen our ecological and evolutionary understanding of lycaenid-ant interactions.

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