

No Experimental Evidence for Host Ant Related Oviposition in a Parasitic Butterfly

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*The ability of adult butterflies of the genus *Maculinea* to locate their host ants prior to oviposition has been the subject of much discussion. We studied the egg laying behavior of the dusky large blue *Maculinea nausithous* whose larvae parasitize colonies of the ant *Myrmica rubra*. Flowerheads of the initial food plant were sprinkled with soil from ant nests, which contain chemicals involved in the nest recognition behavior of ants. The experiment was conducted to determine whether ant-released chemicals may act as oviposition cues and whether intraspecific competition for suitable plants may force female butterflies to alternative decisions. Host plant choice was not influenced by the presence of nest-derived host-ant cues. Density dependent shifts to less suitable host plants could not be ascertained nor changes in egg laying behavior across the flight period. The observed egg distribution could be primarily explained by host plant characteristics and environmental variability among sites. The result confirms the theory that host ant dependent oviposition appears to be a disadvantageous strategy in the face of resource limitation within ant colonies and the immobility of caterpillars.*

KEY WORDS: oviposition; myrmecophily; social parasite; *Maculinea nausithous* .

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INTRODUCTION

The majority of the currently known species of lycaenid butterflies are associated with ants (Fiedler, 1991; Pierce *et al.*, 2002). Most lycaenids have established facultative and obligate mutualisms, a few species exhibit a parasitic life style. In mutualistic relationships ants usually benefit from additional food supplies from lycaenid larvae whereas ants provide enemy free space (e.g. Pierce *et al.*, 1987; Seufert and Fiedler, 1996b; Weeks, 2003; but see Seufert and Fiedler, 1999) or directly enhance the development of butterfly larvae (Fiedler and Hummel, 1996; Wagner, 1993). Parasitic lycaenids enter the ant colonies and either live as predators on the ant brood or are fed by their hosts (Fiedler, 1998). An alternative definition separates predators from parasites including those feeding on ant brood (Pierce, 1995).

Despite the close association of lycaenid larvae to ants adult myrmecophily has been observed in only a few species. A number of obligate myrmecophilous lycaenids are known to prefer ovipositing eggs on host plants within the foraging range of ants (Fiedler, 1993; Fraser *et al.*, 2002; Henning, 1983; Jordano *et al.*, 1992; Pierce and Elgar, 1985; Seufert and Fiedler, 1996a; Seufert and Fiedler, 1996b; Smiley *et al.*, 1988). Ant dependent oviposition can also be found in facultative myrmecophilous lycaenids (Atsatt, 1981; Fiedler and Maschwitz, 1989; Wagner and Kurina, 1997). These references comprise statistically confirmed results, or detailed observations in the case of Henning (1983). For further lycaenid species ant-dependent oviposition has been described or suspected (reviewed by Pierce and Elgar, 1985; Fiedler, 1991).

In our study we focused on butterflies of the genus *Maculinea* which exhibit a highly specialized life style. Adult butterflies oviposit on the inflorescences of a specific food plant. The caterpillars spend only a few weeks on the plant feeding on flowers and developing seeds until they reach the fourth instar. At this stage they leave the plant and are adopted by worker ants of one or more *Myrmica* host ant species (e.g. Als *et al.*, 2002; Elmes *et al.*, 1994; Stankiewicz and Sielezniew, 2002). Inside the ant nests *Maculinea* caterpillars complete their development either feeding on the ant brood or being fed by the worker ants until pupation. The adoption process and the acceptance of caterpillars during their further development is enabled by mimicking the chemical cuticular hydrocarbon profile of ants (Akino *et al.*, 1999; Schlick-Steiner *et al.*, 2004). Given the close relationship between *Maculinea* species and their host ants, one would expect a clear ant-mediated oviposition increasing the probability of being adopted. This has been postulated by Van Dyck *et al.* (2000) whose observations suggest a positive relationship between egg and host ant distribution. A further study combining a field survey with experimental work supports this

argumentation (Wynhoff 2001). However, an alternative theory which emphasizes the importance of host plant traits and habitat characteristics instead of ant presence for oviposition has been proposed by Thomas and Elmes (2001).

Van Dyck and co-workers (2000) observed a higher proportion of eggs laid by *Maculinea alcon* on *Gentiana pneumonanthe* plants within the range of *Myrmica ruginodis* nests than on plants without ant colonies nearby. They suggested a trade off between enhancing the adoption probability and avoiding competition on the host plant because the pattern was restricted to the beginning of the flight period and disappeared when butterfly densities increased. In contrast, Thomas and Elmes (2001) proposed that any correlations between egg laying and the presence of host ants are likely to be the result of heterogeneity in microclimate which affects the phenology of host plants as well as the spatial distribution of ants. They suggested that it would be the best strategy for *Maculinea* butterflies to distribute eggs randomly, to avoid density dependent competition of *Maculinea* larvae within ant colonies. Both studies show that oviposition behavior is affected by an array of environmental variables which might mask existing patterns or lead to the measurement of confounding effects. We chose an experimental approach to be able to distinguish between host ant induced oviposition and indirect effects of habitat heterogeneity. Since *Myrmica* nests are hardly visible in the vegetation we assumed that if female butterflies are able to recognize their host ants they should be geared to olfactory cues. Social insects produce an array of pheromones in their exocrine glands which mainly play a role in colony organization (Billen and Morgan, 1998; Hölldobler and Wilson, 1990). The chemical structure of pheromones is highly diverse and their longevity conforms to the social purpose. Compounds involved in short term behavior such as alarm pheromones are believed to lose their impact after a short time after release (Do Nascimento and Morgan, 1996) and are therefore not appropriate to act as oviposition stimuli for *Maculinea*. In *Myrmica rubra*, the host ant of *Maculinea nausithous*, worker ants establish a specific nest odor using the secretions of their postpharyngeal gland (Cammaerts and Cammaerts, 2000). Experiments showed that small pieces of paper left inside the nests became contaminated with these compounds and caused a behavioral reaction in ants up to 3 h after their isolation from the nests (Cammaerts and Cammaerts, 2000). Other compounds originating from the labial and metapleural glands are involved in the marking of nest entrances and their surrounding area. Similar experimental approaches revealed that the released secretions persist for 15 h (Cammaerts and Cammaerts, 1999). We concluded that soil from *M. rubra* nests should be marked in the same way and we therefore used this soil as

a vector of ant odor. *M. nausithous* oviposits on the flowerheads of *Sanguisorba officinalis* (Rosaceae) which were experimentally manipulated to (1) determine whether *M. nausithous* females preferably choose plants exhibiting information which indicate their proximity to ants, (2) examine the host plant choice on patches inhabiting different butterfly densities (avoidance of competition), and to (3) investigate whether females change their behavior across the flight season.

METHODS

The Oviposition Preference of *M. nausithous*

We performed the experiment at a single location in South Eastern Bavaria (Germany, lat 47°57'N, long 12°51'E). The site comprises three sections which are remarkably different regarding the density of butterflies, their host plants and environmental conditions (Table I). Seventy shoots of *S. officinalis* were selected at each of the three sections of the study site and randomly assigned to two treatment categories, the ant cue treatment, and the control. Plants were chosen in a stratified random manner to minimize the effects of habitat heterogeneity. All flowerheads of the plants were contaminated with soil from *M. rubra* nests and control soil, respectively, to examine whether *M. nausithous* females can locate their host ants by recognizing their odor. Two spoons of soil were applied to each inflorescence ensuring a sufficient amount of particles getting caught between single flowers. This procedure was repeated every second day. Directly

Table I. Characteristics of the Three Investigated Patches

Patch characteristics	Patch 1	Patch 2	Patch 3
Size (m ²)	600	600	1200
Management ^a	2	1	2
Shading	no	no	partly
Vegetation height (SD) ^b	39.8 (4.7)	117.2 (9.8)	54.6 (17.8)
Host plant density (SD) ^c	21.8 (11.9)	13.1 (8.4)	3.3 (4.9)
Butterfly density ^d	1.0	1.1	18.3
Butterfly density ^e	0.17	0.35	22.15

^aNumbers represent the mowing frequency per year.

^bMean vegetation height (cm) was calculated using random 70 replicates per patch.

^cMean density of flowering sprigs (per 4m²) was estimated using 15 sample squares per patch (1 and 2), 30 squares at patch 3.

^dMaximum density of adult butterflies relating to 100m². Butterfly numbers were monitored throughout the experimental period (N = counts)

^eMaximum number of adult butterflies per flowering host plant.

before the treatment started, soil was collected from 5 *M. rubra* colonies and was mixed to avoid possible effects of variation in ant chemistry. For each repeat fresh soil was used. Non-ant soil was obtained in the same way after the absence of ants in the surrounding area of the sampling point had been confirmed. The experiment was started at the onset of the flight period of *M. nausithous* on 5 July 2002. After two weeks when the peak had passed we measured the size of each flowerhead, its phenological stage, and the position in relation to the height of the surrounding vegetation. The phenological stage was determined using 4 categories that described the proportion of open flowers. The position of the flowerheads was measured by dividing them into 3 categories, namely at least 5 cm above or below, or equal to the vegetation. Plants were harvested and the number of eggs and egg shells on each flowerhead was counted in the laboratory.

Statistical Analysis

The number of eggs per flowerhead in relation to soil treatment and host plant traits was analyzed by a generalized linear model (Crawley, 2002). Plants were nested within the combination of treatment and patch. Flowerhead size, phenology, and position were included as covariates. Two way interactions only were considered between treatment and the remaining variables and factors respectively, to investigate whether the discrimination among treatment categories was dependent upon the environmental background or host plant features. Further interactions e.g. between patch and flowering characteristics may also be important. However, to keep the model concise and to focus on the question of ant-dependent oviposition these were given less priority. For the model a Poisson error structure with log link function was chosen. Deviance ratios were checked for significance by comparing with critical values of the *F*-distribution (Rohlf and Sokal, 1995). All analyses were conducted using the software package R version 2.0.1 (<http://www.r-project.org>).

RESULTS

A total number of 1893 eggs were laid on the host plants under study. Thus, the contamination of plants with soil did not prevent oviposition by females. Flowerheads treated with soil from *M. rubra* nests contained an almost similar number of eggs as flowerheads treated with control soil (Fig. 1A). There was no significant difference between treatment categories (Table II). Moreover, all interactions between soil treatment

Table II. GLM Analyzing the Effects of Soil Treatment, Patch, Host plant, Size of Flowerhead, Phenological Stage of Flowerhead, and Position of Flowerhead on the Number of *M. nausithous* Eggs per Flowerhead; Residual deviance = 1554.0 on 1487 Degrees of Freedom; Mean deviance = 1.05

	Df (numerator)	Df (denominator)	Deviance ratio	p
Treatment	1	206	0.34	0.561
Patch	2	206	221.52	< 0.001
Treatment × patch	2	206	0.99	0.373
Treatment × flowerhead size	1	206	0.33	0.566
Treatment × phenology	3	206	0.27	0.847
Treatment × position	2	206	0.002	0.998
Plant	206	1487	5.84	< 0.001
Flowerhead size	1	1487	428.19	< 0.001
Phenology	3	1487	98.57	< 0.001
Position	2	1487	2.76	0.064

and the explanatory variables and factors were not significant (Table II) indicating the independence of the observed pattern from further factors. Importantly, the results were consistent for the three sections of the study site which differed either in adult *M. nausithous* density or the availability of host plants (Table I). Lower butterfly densities on patch 1 and 2 did not lead to increased discrimination among plants from both experimental categories. Further there was no significant interaction between flowering stage and soil treatment. Thus, females exhibited no temporal change in egg laying behavior. Contaminated plants and control plants received similar proportions of eggs across the study period. Oviposition was mainly influenced by patch characteristics and host plant traits (Table II). The widest variation could be explained by the size of *S. officinalis* flowerheads. Females avoided laying eggs on small flowerheads (Fig. 1B). Additionally, the flowering phenology influenced the egg laying pattern of *M. nausithous* (Fig. 1C). At the end of the experimental period most eggs were found on flowerheads containing between one and 50 percent open flowers. The result reflects the preference for a distinct phenological stage, the changing availability of suitable host plants across the flight season, and the consequences arising out of the butterfly phenology. Effects of individual plants also influenced the behavior of *M. nausithous* females. The position of flowerheads in relation to the height of the surrounding vegetation did not play a role in oviposition choice (Table II). However there was a slight tendency towards the selection of more exposed flowerheads which received 1.78 (± 3.50 SD) eggs on average compared to flowerheads located equally to the vegetation (0.60 ± 1.85 SD) or below (0.51 ± 1.76 SD).

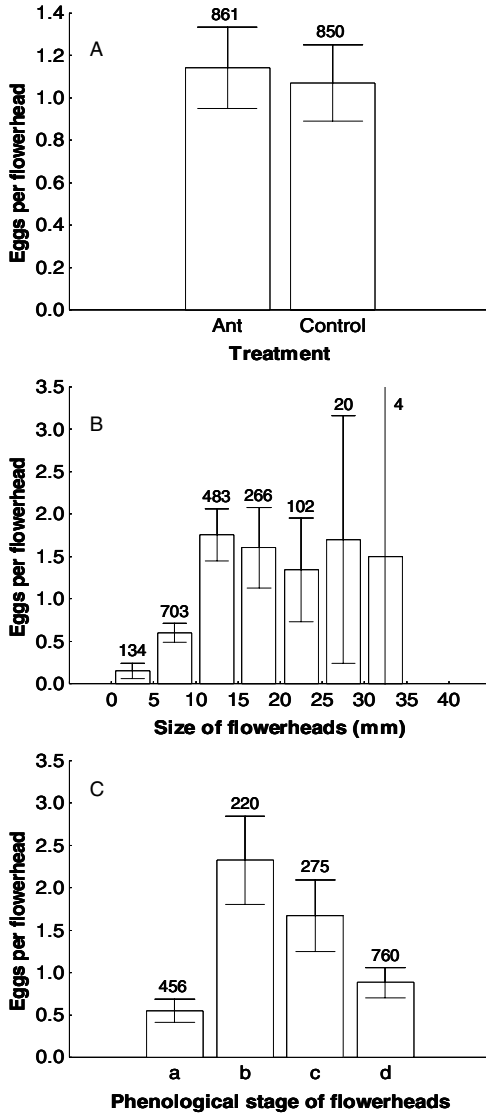


Fig. 1. Mean number of *M. nausithous* eggs per flowerhead (\pm 95% confidence interval, $N = 1712$ flowerheads) in relation to (A) soil treatment, (B) size of flowerheads, and (C) flowering phenology (a = all flowers closed, b = 1%–50% flowering, c = 51%–100% flowering, d = flowerhead wilted). Numbers above columns represent the sample size of flowerheads within the respective category. Statistical results are summarized in table II.

DISCUSSION

The aim of this research was to test whether egg deposition in the genus *Maculinea* is mediated by olfactory cues of the host ants or determined by host plant traits. The result demonstrates the independence of female behavior from nest-derived cues in *M. nausithous*. Instead, the size and phenology of the flowerheads as well as habitat characteristics accounted for the observed egg distribution. These findings support the conclusions drawn by Thomas and Elmes (2001). Accordingly, the limited capacity of an ant colony to enable the successful development of a *Maculinea* larva does not allow the concentration of eggs nearby. Although the chance of a caterpillar being discovered and adopted by a foraging worker ant should be higher in the case of ant related oviposition the subsequent increase of intraspecific competition within ant nests is expected to lower the survival probability. Particularly in the predatory *Maculinea* species to which *M. nausithous* is considered to belong, the early exhaustion of resources would lead to scramble competition (Thomas and Wardlaw, 1992). In this way, populations inhabiting sites with low ant densities would suffer from an enhanced extinction risk.

The positive relationship between host ant presence and egg load on plants observed for *M. alcon* by Van Dyck *et al.* (2000) contrasts with the results of this research. The more efficient feeding strategy of the cuckoo feeder *M. alcon* (Thomas *et al.*, 1993) enables the development of a larger number of larvae per nest than the predacious life style. Recent investigations have revealed caterpillar numbers up to 44 per nest in *M. alcon* (Als *et al.*, 2002). Possibly, the need to avoid overcrowding in the ant nest might not be as essential. However, the restriction of the correlation reported for *M. alcon* to the beginning of the flight period indicates at most a weak relationship with ants but strong interactions with other factors.

As a possible explanation for the lack of correlation at the end of the flight period Van Dyck *et al.* (2000) suggested a shift in female behavior from an initial preference for host plants in the vicinity of ant nests towards plants with lower egg load to avoid intraspecific competition on the plant. Similar conclusions were drawn from a study demonstrating a positive relationship between oviposition and host ant presence in *M. nausithous* and *M. teleius* during the early flight season (Wynhoff, 2001). However, the design of this study allows for a number of alternative explanations. In this present investigation it was found that the oviposition pattern was independent of butterfly density. Therefore it can be concluded that the proposed trade off

between avoidance of competition on the host plant and maximizing the adoption probability does not exist in *M. nausithous*. Generally, low butterfly abundances in relation both to the area covered by the patches and the number of suitable flowerheads available did not lead to an enhanced preference for ant-soil contaminated flowerheads. In addition no interaction between treatment and flowering phenology was found. Thus, females did not change their behavior across the flight season. Butterfly numbers were low at the beginning of the experiment suggesting low competition for host plants during the early flight period. According to the hypothesis of Van Dyck *et al.* (2000) ant dependent oviposition should have occurred at this stage. The subsequent covering of such an early pattern seems to be unlikely since *M. nausithous* prefers a distinct developmental stage for oviposition (Figurny and Woyciechowski, 1998) and the time window for egg laying on a flowerhead is rather short (approximately 2 days). A necessary precondition for the trade off proposed by Van Dyck *et al.* (2000) would be the recognition of conspecific eggs. In contrast to eggs of *M. alcon* which are easily visible on the buds of the *Gentiana* plants, eggs of *M. nausithous* are laid between single flowers and can barely be detected visually by searching females. Although oviposition deterrence on the basis of olfactory cues is a common phenomenon in phytophagous insects (Nufio and Pajaj, 2001) and is also known from a lycaenid butterfly (Rhains, 1996) such a mechanism could not be demonstrated for *M. nausithous* (Figurny and Woyciechowski, 1998).

As already revealed by previous investigations (Figurny and Woyciechowski, 1998; Thomas, 1984) *M. nausithous* females avoided laying eggs on small flowerheads and preferably oviposited on flowerheads being in a medium flowering stage. Large flowerheads promise a higher availability of resources than smaller ones. The selection of early flowering stages ensures that newly hatched larvae are given enough time to pass the first three instars until adoption before seeds mature and flowerheads disintegrate. Further, strong variation in egg numbers was found among patches and individual plants. The patch effect reflects different densities of adult butterflies and host plants what may be the result of variable environmental conditions caused by the respective management regime (Johst *et al.* 2006). Differences in the attractiveness among plants which could not be assigned to the flowering traits may be due to variable plant characteristics such as nutrient content (Baylis and Pierce, 1991; Bourn and Thomas, 1993; Ellis, 2003), or may be influenced by fine-scale microclimatic conditions (Grundel *et al.*, 1998; Roy and Thomas, 2003).

The absence of ant dependent oviposition in *M. nausithous* can be inferred by following the fact that females did not distinguish between

contaminated and control plants. Although there is clear evidence that *M. rubra* ants deposit long lasting chemicals in the vicinity of their nests (Cammaerts and Cammaerts, 1999, 2000) female butterflies also may be geared to highly volatile, short lived compounds which may evaporate rapidly from the test soil. As females search for oviposition sites while flying above the vegetation volatile compounds might be of greater relevance than non volatile ones. Short-lived, volatile compounds can be found for instance in alarm pheromones or trail pheromones (Van der Meer and Alonso, 1998). The latter have been shown to act as oviposition cues, for instance in the lycaenid butterfly *Poecilmitis lycegenes* (Henning, 1983). With respect to this limitation we cannot definitely rule out ant recognition by female *M. nausithous*. Future experimental investigations under laboratory conditions are required to examine the relevance of volatile, ant-released chemicals for oviposition in our study species.

Regardless of the uncertainty concerning the effectiveness of the soil treatment this research corroborates findings from previous research. Comparing the life histories of lycaenids for which ant related oviposition has been confirmed (see Introduction) it can be noted, that apart from *Allotinus unicolor* which preys on homoptera (Fiedler and Maschwitz, 1989) all species are herbivorous and maintain facultative or obligatory mutualistic relationships with ants. In contrast to *Maculinea* butterflies, larvae of these mutualists do not have to cope with limited resources within ant colonies. Therefore, ant-dependent oviposition may be an adequate strategy to ensure a quick establishment of the ant association. In some parasitic lycaenids ant-dependent oviposition has been described or suspected, e.g. *Acrodipsas illidgei* (Beale, 1998), *Cigaritis acamas* (Larsen and Pittaway, 1982), or *Lachnocnema bibulus* (Cripps and Jackson, 1940). These observations suggest that ant dependent oviposition may be a favorable strategy for some parasitic lycaenids, especially for those species exhibiting a mixed feeding style between herbivory and parasitism on ants (classified as “Aphneini type” by Fiedler, 1998), or predation on homoptera and parasitism (“Miletinae type”). However, in the genus *Lepidochrysoptis* which exhibits a similar life style as *Maculinea* observations could not confirm oviposition being related to the presence of host ants (Henning, 1983). At least for this group of parasitic lycaenids (“Maculinea type”) larval survival is strongly limited by the carrying capacity of the ant nests. Thus, it seems to be reasonable that investment in physical structures aiming at the recognition of ant-released chemicals is not worthwhile if there is no benefit in terms of higher survival rates.

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REFERENCES

- Akino, T., Knapp, J. J., Thomas, J. A., and Elmes, G. W. (1999). Chemical mimicry and host specificity in the butterfly *Maculinea rebeli*, a social parasite of *Myrmica* ant colonies. *Proc. R. Soc. Lond. B* **266**: 1419–1426.
- Als, T. D., Nash, D. R., and Boomsma, J. J. (2002). Geographical variation in host-ant specificity of the parasitic butterfly *Maculinea alcon* in Denmark. *Ecol. Entomol.* **27**: 403–414.
- Atsatt, P. R. (1981). Ant-dependent foodplant selection by the mistletoe butterfly *Ogyris amaryllis* (Lycaenidae). *Oecologia* **48**: 60–63.
- Baylis, M., and Pierce, N. E. (1991). The effect of host-plant quality on the survival of larvae and oviposition by adults of an ant-tended lycaenid butterfly, *Jalmenus-evagoras*. *Ecol. Entomol.* **16**: 1–9.
- Beale, J.P. (1998). Temporal and spatial distribution of the rare, myrmecophilous illidge's ant-blue butterfly, *Acrodipsas illidgei* (Lycaenidae). *J. Lepid. Soc.* **52**: 139–150.
- Billen, J., and Morgan, E. D. (1998). Pheromone communication in social insects: sources and secretions. In Vander Meer, R. K., Breed, M. D., Espelie, K. E., and Winston, M. L. (eds.), *Pheromone communication in social insects*, Westview Press, Oxford, pp. 3–33.
- Bourn, N. A. D., and Thomas J. A. (1993). The ecology and conservation of the brown argus butterfly *Aricia agestis* in Britain. *Biol. Conservation* **63**: 67–74.
- Cammaerts, M. C., and Cammaerts, R. (1999). Marking of nest entrances and their vicinities in the ant *Myrmica rubra*. *Biol. (Bratislava)* **54**: 553–566.
- Cammaerts, M. C., and Cammaerts R. (2000). Nest odour in the ant *Myrmica rubra*. *Biol. (Bratislava)* **55**: 509–523.
- Crawley, M. J. (2002). *Statistical computing*. John Wiley and Sons Ltd., Chichester.
- Cripps, C., and Jackson, T. H. E. (1940). The life history of *Lachnocnema bibulus* (Fab.) in Kenya (Lepidopt., Lycaenidae). *Trans R. Ent. Soc. Lond.* **90**: 449–453.
- Do Nascimento, R. R., and Morgan, E. D. (1996). Chemicals involved in the communication system of social insects: their source and methods of isolation and identification, with special emphasis on ants. *Química Nova* **19**: 156–165.
- Eastwood, R., and Fraser, A. M. (1999). Associations between lycaenid butterflies and ants in Australia. *Aust. J. Ecol.* **24**: 503–537.
- Ellis, S. (2003). Habitat quality and management for the northern brown argus butterfly *Aricia artaxerxes* (Lepidoptera Lycaenidae) in North East England. *Biol. Conservation* **113**: 285–294.
- Elmes, G. W., Thomas, J. A., Hammarstedt, O., Munguira, M. L., Martin, J., and Van Der Made, J. G. (1994). Differences in host-ant specificity between Spanish, Dutch and Swedish populations of the endangered butterfly, *Maculinea alcon* (DENIS et SCHIFF.) (Lepidoptera). *Mem. Zool.* **48**: 55–68.
- Fiedler, K., and Maschwitz, U. (1989). Adult myrmecophily in butterflies: the role of the ant *Anoplolepis longipes* in the feeding and oviposition behaviour of *Allotinus unicolor* (Lepidoptera, Lycaenidae). *Tyo to Ga* **40**: 241–251.

- Fiedler, K. (1991). Systematic, evolutionary and ecological implications of myrmecophily within the Lycaenidae (Insecta: Lepidoptera: Papilionoidea). *Bonner Zool. Monogr.* **31**: 1–210.
- Fiedler, K. (1993). The remarkable biology of two Malaysian lycaenid butterflies. *Nature Malaysiana* **18**: 35–43.
- Fiedler, K., and Hummel, V. (1996). Myrmecophily in the brown argus butterfly, *Aricia agestis* (Lepidoptera: Lycaenidae): effects of larval age, ant number and persistence of contacts with ants. *Zoology* **99**: 128–137.
- Fiedler, K. (1998). Lycaenid–ant interactions of the *Maculinea* type: tracing their historical roots in a comparative framework. *J. Insect Conserv.* **2**: 3–14.
- Figurny, E., and Woyciechowski, M. (1998). Flowerhead selection for oviposition by females of the sympatric butterfly species *Maculinea teleius* and *M. nausithous* (Lepidoptera: Lycaenidae). *Entomol. Gener.* **23**: 215–222.
- Fraser, A. M., Tregenza, T., Wedell, N., Elgar, M. A., and Pierce, N. E. (2002). Oviposition tests of ant preference in a myrmecophilous butterfly. *J. Evol. Biol.* **15**: 861–870.
- Grundel, R., Pavlovic, N. B., and Sulzman, C. L. (1998). The effect of canopy cover and seasonal change on host plant quality for the endangered Karner blue butterfly (*Lycaeides melissa samuelis*). *Oecologia* **114**: 243–250.
- Heath, A., and Claassens, A. J. M. (2003). Ant-association among Southern African lycaenidae. *J. Lepid. Soc.* **57**: 1–16.
- Henning, S. F. (1983). Biological groups within the Lycaenidae (Lepidoptera). *J. Entomol. Soc. S. Afr.* **46**: 65–85.
- Hölldobler, B., and Wilson, E. O. (1990). *The ants*. Harvard University Press, Cambridge, Massachusetts.
- Johst, K., Drechsler, M., Thomas, J. A., and Settele, J. (2006). Influence of mowing on the persistence of two endangered large blue butterfly species. *J. Appl. Ecol.* **43**: 333–342.
- Jordano, D., Rodriguez, J., Thomas, C. D., and Haeger, J. F. (1992). The distribution and density of a lycaenid butterfly in relation to *Lasius* ants. *Oecologia* **91**: 439–446.
- Larsen, T. B., and Pittaway, A. R. (1982). Notes on the ecology, biology and taxonomy of *Apharitis acamas* (Klug) (Lepidoptera: Lycaenidae). *Entomol. Gaz.* **33**: 163–168.
- Núño, C. R., and Papaj, D. R. (2001). Host marking behavior in phytophagous insects and parasitoids. *Entomol. Exp. Appl.* **99**: 273–293.
- Pierce, N. E., and Elgar, M. A. (1985). The influence of ants on host plant selection by *Jalmenus evagoras*, a myrmecophilous lycaenid butterfly. *Behav. Ecol. Sociobiol.* **16**: 202–222.
- Pierce, N. E., Kitching, R. L., Buckley, R. C., Taylor, M. F. J., and Benbow, K. F. (1987). The costs and benefits of cooperation between the Australian lycaenid butterfly, *Jalmenus evagoras*, and its attendant ants. *Behav. Ecol. Sociobiol.* **21**: 237–248.
- Pierce, N. E. (1995). Predatory and parasitic Lepidoptera: carnivores living on plants. *J. Lepid. Soc.* **49**: 412–453.
- Pierce, N. E., Braby, M. F., Heath, A., Lohman, D. J., Mathew, J., Rand, D. B., and Travassos, M. A. (2002). The ecology and evolution of ant association in the Lycaenidae (Lepidoptera). *Annu. Rev. Entomol.* **47**: 733–771.
- Rhainds, M., Gries, G. and Morales, J. L. (1996). Oviposition deterrence in pineapple borer females, *Thecla basilides* (Lepidoptera: Lycaenidae). *Ecol. Entomol.* **21**: 105–106.
- Rohlf, J. F., and Sokal, R. R. (1995). *Statistical tables*, Freeman, New York.
- Roy, D. B., and Thomas, J. A. (2003). Seasonal variation in the niche, habitat availability and population fluctuations of a bivoltine thermophilous insect near its range margin. *Oecologia* **134**: 439–444.
- Schlick-Steiner, B. C., Steiner, F. M., Höttinger, H., Nikiforov, A., Mistrík, R., Schafellner, C., Baier, P., and Christian, E. (2004). A butterfly's chemical key to various ant forts: intersection-odour or aggregate-odour multi-host mimicry? *Naturwissenschaften* **91**: 209–214.
- Seufert, P., and Fiedler, K. (1996a). The influence of ants on patterns of colonization and establishment within a set of coexisting lycaenid butterflies in a south-east Asian tropical rain forest. *Oecologia* **106**: 127–136.

- Seufert, P., and Fiedler, K. (1996b). Life history diversity and local co-existence of three closely related lycaenid butterflies (Lepidoptera: Lycaenidae) in Malaysian rain forests. *Zool. Anz.* **234**: 229–239.
- Seufert, P., and Fiedler, K. (1999). Myrmecophily and parasitoid infestation of South-East Asian lycaenid butterfly larvae. *Ecotropica* **5**: 59–64.
- Smiley, J. T., Atsatt, P. R., and Pierce, N. E. (1988). Local distribution of the lycaenid butterfly, *Jalmaenus evagoras*, in response to host ants and plants. *Oecologia* **76**: 416–422.
- Stankiewicz, A., and Sielezniew, M. (2002). Host specificity of *Maculinea teleius* BGSTR. and *M. nausithous* BGSTR. (Lepidoptera: Lycaenidae) The new insight. *Ann. Zool.* **52**: 403–408.
- Thomas, J. A. (1984). The behaviour and habitat requirements of *Maculinea nausithous* (the dusky large blue butterfly) and *Maculinea teleius* (the scarce large blue butterfly) in France. *Biol. Conserv.* **28**: 325–347.
- Thomas, J. A., and Wardlaw, J. C. (1992). The capacity of a *Myrmica* ant nest to support a predacious species of *Maculinea* butterfly. *Oecologia* **91**: 101–109.
- Thomas, J. A., Elmes, G. W., and Wardlaw, J. C. (1993). Contest competition among *Maculinea rebeli* butterfly larvae in ant nests. *Ecol. Entomol.* **18**: 73–76.
- Thomas, J. A., and Elmes, G. W. (2001). Food-plant niche selection rather than the presence of ant nests explains oviposition patterns in the myrmecophilous butterfly genus *Maculinea*. *Proc. R. Soc. Lond. B* **268**: 471–477.
- Van Der Meer, R. K., and Alonso, L. E. (1998). Pheromone directed behavior in ants. In Vander Meer, R. K., Breed, M. D., Espelie, K. E., and Winston, M. L. (eds.), *Pheromone communication in social insects*, Westview Press, Oxford, pp. 3–33.
- Van Dyck, H., Oostermeijer, J. G. B., Talloen, W., Feenstra, W., Van der Hidde, A., and Wynhoff, I. (2000). Does the presence of ant nests matter for oviposition to a specialized myrmecophilous *Maculinea* butterfly? *Proc. R. Soc. Lond. B* **267**: 861–866.
- Wagner, D. (1993). Species-specific effects of tending ants on the development of lycaenid butterfly larvae. *Oecologia* **96**: 276–281.
- Wagner, D., and Kurina, L. (1997). The influence of ants and water availability on oviposition behaviour and survivorship of a facultative ant-tended herbivore. *Ecol. Entomol.* **22**: 352–360.
- Weeks, J. A. (2003). Parasitism and ant protection alter the survival of the lycaenid *Hemiargus isola*. *Ecol. Entomol.* **28**: 228–232.
- Wynhoff, I. (2001). At home on foreign meadows: the reintroduction of two *Maculinea* butterfly species. Doctoral thesis. Wageningen Agricultural University.