Ecological Entomology (2009), **34**, 90–97 DOI: 10.1111/j.1365-2311.2008.01048.x

Oviposition preferences of *Maculinea alcon* as influenced by aphid (*Aphis gentianae*) and fungal (*Puccinia gentianae*) infestation of larval host plants

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Abstract. 1. The influence of infestation of the larval host plant *Gentiana cruciata* on the egg-laying preferences of the xerophilous ecotype of Alcon Blue butterfly (*Maculinea alcon*) was studied in a semi-dry grassland area (Aggtelek Karst Region, Northern Hungary).

2. We examined whether oviposition patterns of females differed when *G. cruciata* stems were uninfested compared with when they were infested by an aphid (*Aphis gentianae*) or a rust (*Puccinia gentianae*) species.

3. Females laid more than 90% of their eggs on fertile, uninfested *G. cruciata* stems, although these stems comprised only ∼ 50% of the total stems available. Stems infested by aphids were similar to uninfested ones in properties that had a strong correlation with egg numbers, and yet there were significantly fewer eggs on infested stems than on intact ones.

4. Females never laid eggs on parts of *Gentiana* stems infested by aphids, and the presence of *Lasius paralienus* ants, which have a mutualistic interaction with *Aphis gentianae*, did not increase the repulsive effect of aphids. Infection of *Gentiana* by *Puccinia* did not influence the egg-laying behaviour of females, even though the flowers and buds of infested stems exhibited a delayed development.

5. Aphid infestation can influence butterfly oviposition patterns through both direct and indirect effects. The presence of aphids directly excluded oviposition, but our data also indicated the possibility of an indirect effect of aphid infestation. Stems that had no aphids at the last egg counting, but were infested prior to it, had significantly fewer eggs than those that were never infested.

Key words. Aggtelek National Park, Alcon Blue, *Gentiana cruciata*, infestation by aphids and rust, oviposition behaviour.

Introduction

As a result of their unusual life cycle and conservation status, *Maculinea* butterflies (Lepidoptera: Lycaenidae) have attracted considerable research attention (Elmes & Thomas, 1987, 1992; Munguira & Martin, 1997; Wynhoff, 1998; Van Swaay & Warren, 1999). Their larvae initially feed on specific larval host plants, followed by development in the nests of *Myrmica* (Hymenoptera: Formicidae) host ants. Both the larval host plant and the host ant are indispensable for the successful development of *Maculinea* species. Larvae will die if they cannot reach fruit capsules after hatching (H. Malicky, pers. comm. and our unpublished data) or if they subsequently fail to be adopted by ants (Elmes *et al.*, 1991). As a consequence, it is essential for the female to select the optimal food plant for laying her eggs. In order to examine factors influencing egg-laying preferences, it is important to study how the presence of other species feeding on *Gentiana* (e.g. aphids) may affect butterfly oviposition behaviour.

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In the past few years, several authors have studied the egg-laying preference of *Maculinea alcon*. According to some reports, one of the most important factors influencing oviposition is the distance between the larval host plant and the host ants' nest (Scheper *et al.*, 1995; Van Dyck *et al.*, 2000). However, other authors have found no correlation between egg numbers and the presence of ant nests (Thomas & Elmes, 1998, 2001). The potential effects of other characteristics of the food plant on the behaviour of females have also been studied (Thomas & Elmes, 2001; Küer & Fartmann, 2005; Nowicki *et al.*, 2005; Árnyas *et al.*, 2006). Although some specific pathogen species of *Gentiana* have been known for a considerable period of time (Parmelee & deCarteret, 1985; Tomanović *et al.*, 2003; Kavallieratos *et al.*, 2004), their effects on the egg-laying preferences of females have not previously been considered.

In our survey area on the Tohonya ridge (Aggtelek Karst Region, Northern Hungary; site description in Árnyas *et al.*, 2006), *Gentiana cruciata* L. stems were occasionally infested by aphids and rust, which gave us the opportunity to investigate whether these infestations affected oviposition patterns of *M. alcon* females. We examined relationships between the numbers and location of eggs and the abundance of aphids and incidence of rust.

In the analyses of the data, we had several hypotheses to test. Our first assumption was that the aphid and rust species had a similar and negative effect on the egg-laying behaviour of females. Our second hypothesis was that the presence of aphid and rust species had a derived effect on oviposition by reducing the quality of *Gentiana* stems, and consequently reducing their attractiveness to females. We compared characteristics of infested and intact fertile *Gentiana* stems in order to examine factors affecting stem selection for oviposition by the butterfly.

Materials and methods

Investigated species

The xerophilous ecotype of *Maculinea alcon* [(Denis et Schiffermüller), 1775] (=*Maculinea rebeli* auct. nec Hirschke, 1904, see: Kudrna, 2001; Kudrna & Belicek, 2005) is widespread in the western part of the Palaearktis (Hesselbarth *et al.*, 1995; Munguira & Martin, 1997; Wynhoff, 1998; Van Swaay & Warren, 1999; Als *et al.*, 2004). In Hungary, it occurs sympatrically but not syntopically together with the marsh ecotype (Bereczki *et al.*, 2005, 2006). The flight period of the xerophilous ecotype is between the second week of June and the third week of July (Bálint, 1996; Peregovits *et al.*, 2001; Árnyas *et al.*, 2005). It occurs locally in the Northern and Trans-Danubian Mountains, but occasionally may have strong populations on semi-dry meadows and calcareous grasslands, where *G. cruciata* is abundant.

Gentiana cruciata is widespread across the whole continent. It grows in clumps consisting of several (1–14) stems of varying heights up to 40 cm. Its flowering period lasts from the end of June to early September. In our study area, in addition to the butterfly, there are two other species found feeding occasionally on *G. cruciata*; an aphid species, *Aphis gentianae* Börner, 1940 (Sternorrhyncha: Aphididae) and a leaf rust pathogen, *Puccinia gentianae* (Strauss) Röhl., 1813 (Uredinales: Pucciniaceae). Although their occurrence has been known in the Carpathian basin, no earlier data has been published from Hungary so far. Aphids always occurred on the protected parts of whorls on *Gentiana* stems (mostly at the bases of leaves and flowers and on the abaxial surfaces of leaves). The uredia of *Puccinia* mostly occurred on the leaf lamina of the infested stems.

Study area

The study site is an area of approximately 3 hectares on a gently sloping ridge between the valleys Tohonya and Lófej, north of the village of Jósvafő. The site is a managed (transitional) zone of the Aggtelek National Park and Biosphere Reserve (see Árnyas *et al.*, 2006 for a description of the site).

The process of sampling

Initially, a 7500m^2 sampling area was selected within the 3 ha habitat. This area of 7500 m^2 was then subdivided into 10×10 m squares. 40, 50 and 20 of these squares were then randomly selected for investigation in 2004, 2005, and 2006, respectively. In 2004, five squares where stems were infested by aphids were found, while in 2005, infested stems occurred in six squares. As the number of infested stems was very low, we merged the data for these 2 years in our subsequent analyses. In 2006, 14 out of 20 squares had stems, infested by aphids. Our subsequent analyses only consider those squares with infested stems.

Our investigations were carried out during the second half of the flight period of *M. alcon*. The following data were recorded for each square: (i) the numbers and types of stems in clumps of *G. cruciata* (intact fertile, intact sterile, grazed, infested by aphids or rust) (2004, 2005, 2006), (ii) the heights of the stems and the surrounding vegetation (2005, 2006), (iii) the numbers of whorls with flowers (2004, 2005, 2006), (iv) the numbers of eggs on the different whorls of the stems (2004, 2005, 2006). In 2006, (v) the numbers of the flowers and buds and their phenological stages, and (vi) the number of aphids and *Lasius* ants on the stems were also recorded. Furthermore in 2006, records were taken three times of the numbers of butterfly eggs and aphids on stems (at 8 day intervals) during the flight period of *M. alcon*.

Statistical analyses

In order to normalise data, when necessary, we calculated abundance of butterfly eggs and aphids as log $(n + 1)$. In testing the derived effect hypothesis (i.e. the assumption that the presence of aphid and rust species affects oviposition by reducing the quality of *Gentiana* stems), analysis of variance (ANOVA) was used (Michaletzky, 1986), where stem types were examined in relation to the following variables: numbers of eggs, numbers of whorls with flowers, prominence of *G. cruciata* stems above the surrounding vegetation, and the numbers of flowers and buds. Paired comparisons were performed using Tukey–Kramer tests (Sokal & Rohlf, 1995). As the recorded characteristics of

Gentiana stems are in strong correlation with each other (Árnyas *et al.*, 2006) a partial correlation was carried out between egg numbers and the other variables measured, followed by stepwise multiple linear regression (Székely, 1986) in order to find the most significant factors in females' host plant choice. When studying interactions between egg numbers and the phenological stages of stems, both variables were coded categorically as follows: egg numbers: 1: ≤ 10, 2: 11–20, 3: ≥ 21; phenological stages of stems: (i) mostly buds, (ii) equal number of buds and flowers, and (iii) mostly flowers, and analysed using a χ^2-test (Crawley, 1993). In analyses of interactions between the numbers of eggs and aphid abundance (i.e. tests of direct effects of aphids on oviposition), stems were allocated to one of two categories: eggs – 1 = stems with eggs, 2 = stems without egg; aphids – 1 = stems with aphids, 2 = stems without aphids, and analysed using a χ^2-test (Crawley, 1993). In order to investigate any indirect effects of aphid infestation on the ovipositing behaviour of females, we compared egg numbers among all stems that were infested by aphids at any of the three sampling occasions. Specifically, we calculated the proportion of stems with eggs among those ones that had no aphids at the third (main) sampling occasion, but were infested earlier. We then compared this ratio with the proportion of stems with eggs among all fertile ones using Fisher's exact test. All statistical analyses were performed with the SPSS 14.0 programme package (Ketskeméty & Izsó, 2005; Norusis, 2006).

Results

Exploration of basic data

In 2004 and 2005, a total of 134 *G. cruciata* clumps was found in the 11 squares, where stems infested with aphids had been detected. In 2006, 94 clumps were counted in the 14 squares surveyed. The distribution of the different stem types was similar in the two study periods (Fig. 1). Most of the stems were intact and fertile, and only a small portion of them were infested by aphids. Aphid infestation was observed in both time periods, whereas stems infected by rust were only found in 2006 (Fig. 1).

In both time periods, significant differences were found between the stem types in terms of the numbers of eggs on them (ANOVA, 2004–05: $F_{3,517} = 170.727$, $P < 0.001$; 2006: $F_{4,450} = 55.887$, $P < 0.001$). Females laid more than 90% of their eggs on intact fertile uninfested stems (2004–2005: 97.90%; 2006: 92.72%) despite the fact that these stems amounted to only slightly more than 50% of the total number of stems (2004–2005: 60.65%; 2006: 57.15%). Intact fertile stems had significantly more eggs on them than did aphid-infested, intact, sterile and grazed stems. However, no significant differences were found between the intact fertile and rust infested stems (Table 1).

Consequences of aphid infestation: derived effect hypothesis

We first examined whether there was a kind of indirect effect (later it is referred to as derived effect) of aphid infestation on egg number, i.e. if aphids depleted the quality of infested stems, which in turn became less attractive for the females to oviposit on them. In order to test this, a multiple regression model was computed to determine the most important characteristics of stems in oviposition. This analysis showed that the number of fertile whorls and the prominence of stems from the surrounding vegetation was significantly positively related to egg numbers, whereas the number of aphids on stems was significantly negatively related to egg numbers. The number of flowers and buds and the height of stems did not significantly influence the numbers of eggs (Table 2).

In the next analysis, the five different stem types were compared in terms of differences in the morphological characteristics that were correlated with egg numbers. The results indicated significant differences among stem types in terms of the numbers of fertile whorls present in either time period (ANOVA; 2004–05: $F_{3,517} = 252.204$, $P < 0.001$; 2006: $F_{4,450} = 192.039$, $P < 0.001$), although no significant differences were detected between intact fertile stems and ones infested with aphids in 2004–05 (Fig. 2a). Moreover, the significant difference among stem types found in 2006 clearly showed that infested stems had more fertile whorls than the ones free from aphids (Fig. 2a). There were no

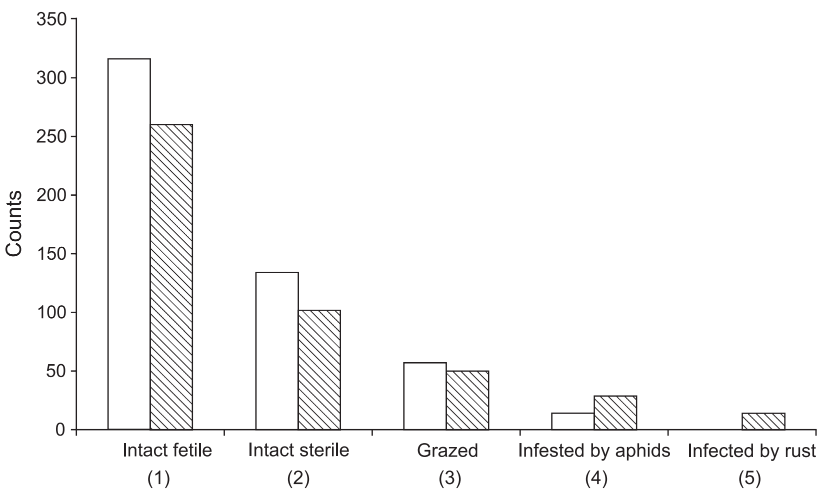

Fig. 1. Distribution of different stem types in the two study periods. Empty bars: 2004–05; hatched bars: 2006.

Table 1. Mean number of eggs (± SE) on five different stem types in the two study periods. Sample sizes are in brackets: 2004–05/2006.

Stem types	2004–05	2006
Intact fertile (316/260)	11.23 ± 0.612	6.71 ± 0.575
Intact sterile (134/102)	0.00 ± 0.000	0.00 ± 0.000
Grazed (57/50)	0.75 ± 0.306	0.40 ± 0.206
Infested by aphids (14/29)	2.36 ± 1.369	1.62 ± 0.844
Infected by rust (0/14)	—	5.00 ± 1.501

significant differences in the numbers of fertile whorls between intact fertile stems and stems infested by rust (Fig. 2a).

Stem types also differed in terms of prominence from the surrounding vegetation in both time periods (2004–05: $F_{3,368} = 88.45$, $P < 0.001$; 2006: $F_{4,450} = 216.305$, $P < 0.001$). However, intact fertile stems and those infested by aphids or rust did not differ in prominence (Fig. 2b).

As neither of these morphological characteristics explained any differences in the numbers of eggs laid on intact-fertile stems and those infested by aphids and rust, further stem parameters were analysed. This revealed that most characteristics of *Gentiana* stems were significantly correlated with egg numbers when variables were entered separately into analysis (Table 3).

The numbers of flowers and buds on stems, and their phenological stages were studied in 2006. Intact fertile stems had significantly fewer flowers and buds than stems infested by aphids (ANOVA, $F_{4,386} = 49.995$, $P < 0.001$; Fig. 2c), although there were no differences between intact fertile stems and those infested by rust (Fig. 2c). Intact fertile stems also had significantly more flowers in bloom than those infested by rust (ANOVA, $F_{4,386} = 22.489$, $P < 0.001$; Fig. 2d), although there were no significant differences between intact fertile and aphid-infested stems (Fig. 2d). Thus, the phenological stage of stems seems to have been affected more by rust infection than by aphids.

Consequences of aphid infestation: direct effect hypothesis

We then examined whether aphids affected oviposition behaviour directly. In 2006, an extensive survey was performed on the effects of aphids on egg numbers. A contingency table was used in which data for all fertile stems were included. Stems were classified according to the presence of eggs and aphids on them. The presence of eggs was not independent of the presence of aphids ($\chi^2_1 = 11.4$, $P = 0.001$), i.e. the presence of aphids on a stem decreased the probability of the occurrence of eggs (Fig. 3). There were only 12 stems with eggs that were also infested with aphids, but in most of these cases, aphids and eggs appeared on different whorls. Aphids and eggs only appeared on the same whorl in 5 out of 96 cases, and so we conclude that there is a direct inhibitory effect of aphids on oviposition.

Consequences of aphid infestation: indirect effect hypothesis

We examined whether the earlier presence of aphids had a subsequent effect on later oviposition. We compared the number of eggs on stems which had no aphids at the third sampling time (even though they had been infested earlier), with the number of eggs on all fertile stems. The results of Fisher's exact test showed that the frequency of stems with eggs was significantly lower among the stems which were earlier infested by aphids, than among the intact fertile ones ($\chi^2_1 = 6.01$, $P < 0.05$). This indicates that in addition to their direct inhibitory effect, aphids also have an indirect effect on oviposition.

Effect of attending ants

In 2006, *Lasius paralienus* ants were detected on 11 out of 29 stems infested by aphids. The rate of infestation by aphids was correlated with the numbers of ants on stems ($r = 0.656$, $n = 29$, $P < 0.001$) (Fig. 4). However, there was no significant differences in egg numbers between stems with aphids and ants, and those stems with aphids only (2006: $t_{27} = 0.766$, $P > 0.05$).

Consequences of rust infection

Rust-infected stems were generally rare in the study area but were sufficiently abundant to carry out analyses in 2006. The effect of rust infection on egg numbers was investigated using

Table 2. The influence of various morphological characteristics of *Gentiana* stems (both in 2004–05 and in 2006: number of fertile whorls, prominence of stems, height of stems; in 2006 only: number of aphids, number of flowers and buds) on the number of eggs laid. Results show output from forward stepwise multiple linear regression [numbers of eggs and aphids are expressed as log ($n + 1$)].

	Independent variables	Coefficient *B*	SE	*t*	*P*
2004–05	Number of fertile whorls	0.417	0.025	16.866	***
	Prominence of stems	0.010	0.004	2.353	*
	Height of stems	—	—	0.353	n.s.
2006	Number of fertile whorls	0.153	0.029	5.211	***
	Number of aphids	–0.325	0.064	–5.101	***
	Prominence of stems	0.019	0.005	3.698	***
	Height of stems	—	—	0.998	n.s.
	Number of flowers and buds	—	—	0.093	n.s.

SE = standard error, ***$P < 0.001$, *$P < 0.05$, NS = not significant.

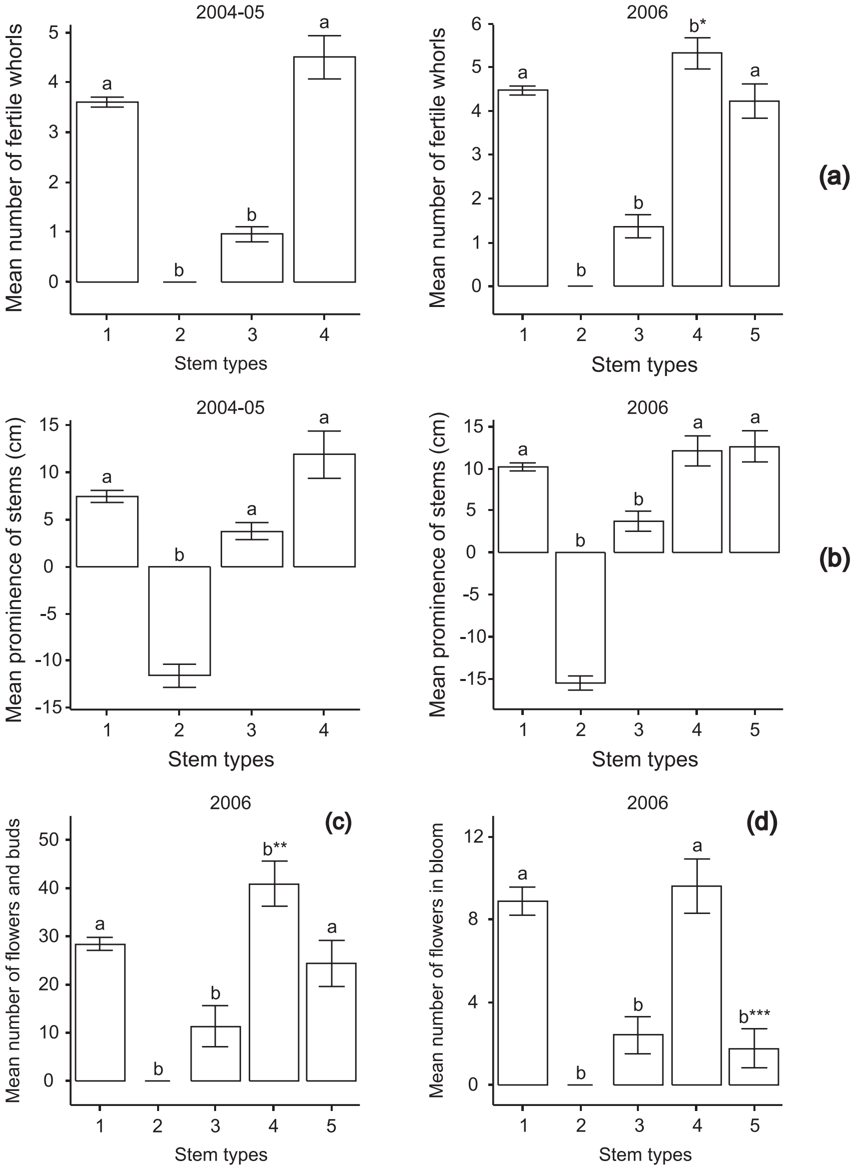

Fig. 2. Mean number of fertile whorls (±SE) (a), mean prominence (±SE) (b), average number of flowers and buds (±SE) (c) and mean number of flowers in bloom (±SE) (d) on different stem types. (i) intact fertile, (ii) intact sterile (iii) grazed, (iv) infested by aphids, (v) infected by rust. All stem types were compared with the intact fertile one (first column) using Tukey–Kramer test. Letters above the columns indicate levels of significance: a, no significant difference; b, $P < 0.001$; b*, $0.01 < P < 0.05$; b**, $0.001 < P < 0.01$.

contingency tables, and all stems were categorised on the basis of occurrence of eggs and rust infection. There was no effect of rust infection on egg number ($\chi^2_1 = 0.96$, $P = 0.32$).

Discussion

The distribution of butterfly eggs on *Gentiana* was not equal among stems (Peregovits *et al.*, 2001; Küer & Fartmann, 2005). Our findings confirmed that tall intact fertile stems were the most attractive to females. Significantly fewer eggs were laid on stems infested by aphids, whereas infection by rust did not affect oviposition. The results of the multiple regression analysis confirmed that the number of whorls with flowers/flower buds and the prominence of the stems from the surrounding vegetation, were two important factors affecting oviposition (Árnyas *et al.*, 2006), as has also been shown to be important for oviposition in the marshland ecotype of *M. alcon* (Küer & Fartmann, 2005; Nowicki *et al.*, 2005).

Table 3. Pearson's correlation between the number of eggs laid [expressed as log $(n + 1)$] and different morphological variables of *Gentiana* stems.

Parameters	*N*	*r*	*P*
Number of fertile whorls	455	0.482	***
Height of stems	455	0.471	***
Prominence of stems	455	0.444	***
Number of flowers and buds	391	0.402	***
Number of flowers in bloom	391	0.350	***

$^{***}P < 0.001$.

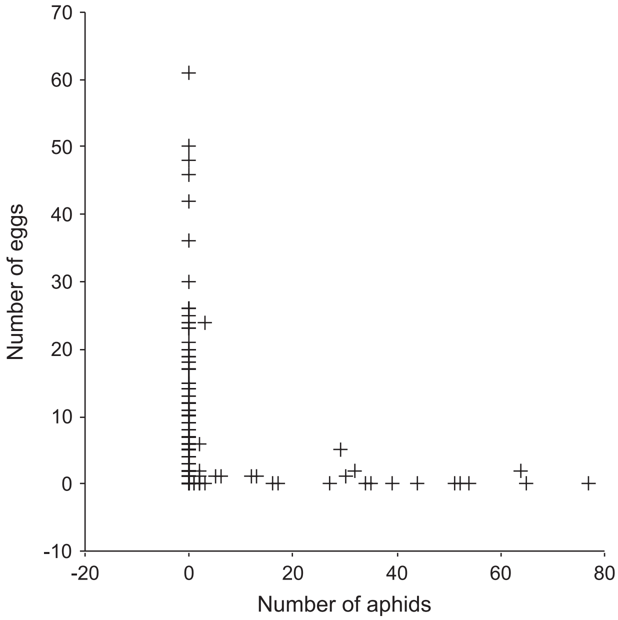

Fig. 3. Correlations between the number of *Maculinea* eggs and the number of aphids on the plants. ($r = -0.244$, $n = 289$, $P < 0.001$).

Significantly fewer eggs were laid on the aphid-infested stems than on the intact ones, suggesting that the presence of aphids (*A. gentianae*) directly inhibits oviposition by the butterfly. There are two possible ways this inhibition might act: via a direct or an indirect effect. First we considered that aphids have a direct, actual physical effect on ovipositing females. If this hypothesis were true, we would never find eggs on aphid-infested whorls. On the whole, our findings supported the direct inhibition hypothesis, because eggs and aphids were observed almost exclusively on different whorls, although they appeared together on only 5% of the whorls surveyed. When eggs and aphids occurred on the same whorls, eggs were always found on the adaxial surface of leaves, whereas aphids were on the abaxial surface, thus avoiding direct contact between the aphids and the egg-laying females.

Evidence for indirect effects of aphids on oviposition was also examined. Females only ovipositied on 46% of the fertile stems that had previously been infested by aphids, whereas eggs were on a total of 69% of all intact fertile stems. As these infested stems did not have aphids on them at the time eggs were counted, it was assumed that the earlier infestation had affected the ovipositing behaviour of females.

It is well known that there is a mutualistic interaction between aphids and some ant species (Flatt & Weisser, 2000 and references therein). Aphids secrete energy-rich nutrients (honeydew), and in exchange for these nutrients, ants decrease the impact of predators and parasitoids on their hosts (Volkl, 1992 and references therein). In this study, it is clearly shown that the presence of attending ants did not affect the repulsive effect of aphid infestation. We conclude that the presence of aphids alone inhibits oviposition both through direct and indirect effects on oviposition.

In contrast with aphids, infection by *Puccinia* rust had little impact on oviposition. Stems infected by rust did not differ significantly from intact fertile ones in terms of all morphological variables measured and numbers of eggs laid. The only factor, which differed significantly between intact fertile stems and the ones infected with rust, was the phenological stage of flowers and buds. The portion of flowers was lower on stems infected by rust than on intact fertile ones, although this did not influence the numbers of eggs laid. This observation differs from other work, showing that oviposition patterns of *Maculinea 'rebeli'* mostly depend on the availability of suitable phenophase of flowers and flower buds on *Gentiana* plants (Thomas & Elmes, 2001). There are several possible explanations for this apparent difference between the results of the two studies. First, the flowering period of *G. cruciata* is at least twice as long as the flight period of *M. alcon.* Our study period was set according to the interval Alcon Blues were on wing, while that of Thomas and Elmes (2001) was adjusted to the flowering period of *G. cruciata*. Second, the interaction between the phenological stages of flowers and the egg-laying behaviour of females is fairly complicated, as two cumulative processes have to be considered: (i) a continuous shift of the portion of buds and flowers in bloom and (ii) the increasing number of eggs on the shoots. Accordingly, the correlation between the phenophase of *Gentiana* flowers

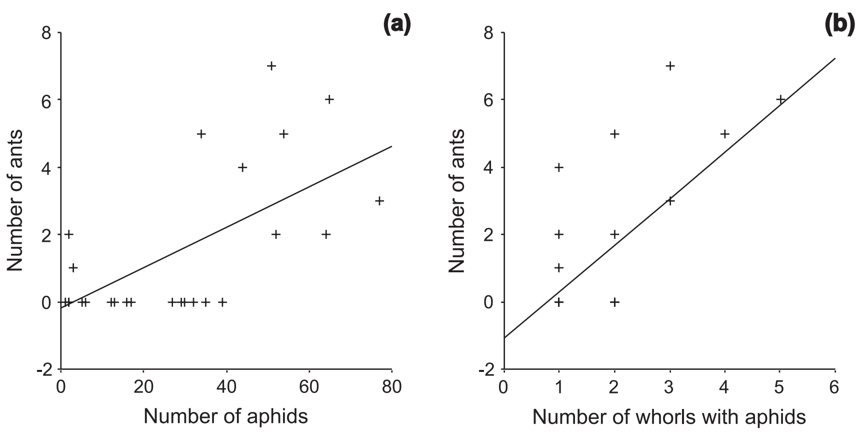

Fig. 4. Correlations between the number of *Lasius* ants and the number of aphids (a), respectively the numbers of whorls with aphids (b).

and the oviposition preference of *Maculinea* females may have local differences. Our results provide indirect evidence that buds, which make up a large portion of rust-infected stems, are not particularly favoured by females for oviposition. Females, especially late flying ones, also laid eggs on flowers in bloom, as the number of eggs increased in a cumulative manner, together with a shift of the phenological stage of stems. Therefore, there may be some plasticity in the oviposition preferences of *M. alcon* in terms of stem phenology, and this plasticity could be important for the survival of the butterfly under extreme weather conditions.

Acknowledgements

This study was supported by the EU EVK2-CT-2001-00126 (MacMan) and NKFP-3 B/023/2004 projects. We would like to express our thanks to Zs. Basky for the identification of the aphid species (*Aphis gentianae*) on *Gentiana cruciata.* The authors are grateful to I. Wynhoff, J. Settele, J. Hill and to all anonymous referees for many useful suggestions, which have greatly improved the manuscript. We would like to express our special gratitude to the management of Aggtelek National Park for their assistance in our investigations.

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Accepted 10 June 2008
First published online 17 October 2008