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Does the presence of ant nests matter for oviposition to a specialized myrmecophilous *Maculinea* butterfly?

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More than 50% of the lycaenid butterflies have an ant-associated lifestyle (myrmecophily) which may vary from coexistence to specific mutualistic or even parasitic interactions. Ant-related host-plant selection and oviposition has been observed in some myrmecophilous lycaenids. Therefore, it is remarkable that there is no evidence for this behaviour in the highly specialized, obligate myrmecophilous butterflies of the genus *Maculinea*. In contrast with previous findings, our results provide evidence for ant-related oviposition patterns in *Maculinea alcon* in relation to the distribution of specific host-ant nests (i.e. *Myrmica ruginodis*) based on repeated egg counts during the flight period in two populations. We also show that ant-related oviposition can be counterbalanced by intraspecific competition and oviposition deterrency when host plants already carry several eggs. Therefore, the absence of a correlation between egg load and the presence of host-ant nests at the end of the flight period should be interpreted carefully. Whether ovipositional cues are obtained either directly (from ants or their nests) or indirectly (from vegetation structure), and whether alternative explanations based on the phenology and growth form of host plants are possible, is discussed.

Keywords: oviposition; myrmecophily; ants; butterflies; *Maculinea alcon*

1. INTRODUCTION

Myrmecophily or an ant-related lifestyle is known worldwide in (among other insects) more than 50% of the lycaenid butterflies, including a range of associations from coexistence to mutualistic or even parasitic interactions (Fiedler 1991; Fiedler *et al.* 1996). Mostly it concerns a mutualistic relationship in which larval secretions provide energetic rewards for the ants while the larvae benefit from protection from parasitoids and arthropod predators, including the ants themselves (Pierce 1989; Cushman *et al.* 1994; Fiedler *et al.* 1996). Myrmecophily may affect different life-history aspects, including mate location, size and/or fecundity, dispersal and oviposition (Fiedler 1997). In order to generate ecologically specialized life-history phenotypes, a strong selection on oviposition site choice is expected, comparable to selection on 'hard' life-history components (e.g. egg size and number) (Resetarits Jr 1996). Since the mobility of lycaenid larvae is usually very limited, ant-related host-plant selection and oviposition by females—and hence a spatial correlation between eggs or larvae and host ants—is expected, and confirmed in some myrmecophilous species (e.g. Pierce & Elgar 1985; Jutzeler 1989; Fiedler 1991; Jordano *et al.* 1992; Seufert & Fiedler 1996).

Butterflies of the genus *Maculinea* are obligately myrmecophilous and depend fully on *Myrmica* ants for survival. After a short feeding period on the host plant, caterpillars are adopted by the ants and live most of their life in the colony feeding on ant brood (i.e. *Maculinea arion*, *Maculinea teleius* and *Maculinea nausithous*) or being fed by worker ants (i.e. *Maculinea alcon* and *Maculinea rebeli*) (Thomas *et al.* 1998). Knowing that ant-dependent oviposition occurs in some lycaenids, that each *Maculinea* species survives mainly with a specific *Myrmica* species (Thomas *et al.* 1989), and that caterpillars passively wait for adoption (Elmes & Thomas 1987), it seems remarkable that there is no evidence (despite old observations reported in Pierce & Elgar (1985)) for oviposition patterns that match host-ant distribution in these extremely specialized butterflies (Thomas 1984; Thomas *et al.* 1989; Elmes *et al.* 1991; Clarke *et al.* 1998; but see preliminary data on *M. alcon* in Scheper *et al.* (1995)). In this vein, oviposition and the establishment of the correct ant association in *Maculinea* is considered a random process (Fiedler 1991).

A possible explanation for the apparent random pattern is that selection on ant-related oviposition may be (partly) counterbalanced by, among other factors, oviposition deterrency. The pay-off for laying an additional egg on an overcrowded host plant with a high adoption probability (i.e. within the range of one or more host-ant nests) could approximate the success of ovipositing on an 'empty' host plant with a lower adoption chance but also less competition with other larvae. Such a trade-off between adoption chance and intraspecific competition may result in a temporal shift in oviposition preference. Hence, counting eggs at the end of the flight season may reveal no or only a weak overall correlation between egg and host-ant distribution. It is known in Lepidoptera that

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competition among females for oviposition sites leads to a more uniform egg distribution than would occur without competition (Thompson & Pellmyr 1990).

M. alcon caterpillars compete for food both in the flowers and in the ant nest after adoption. Caterpillar mass (when leaving the host plant) is significantly lower at higher egg densities (Gadeberg 1997). This is an important density-dependent larval fitness component since the probability of adoption and the subsequent survival is higher for heavier caterpillars. Density-dependent mortality may also occur on the host plant (cf. *M. rebeli* G. W. Elmes, J. A. Thomas and J. C. Wardlaw (unpublished results) in Hochberg *et al.* (1992)), but remains to be examined in *M. alcon*. Once adopted, caterpillars experience contest competition in the ant nest (Thomas *et al.* 1993). Since *Myrmica* ants adopt caterpillars regardless of the number that have been adopted before, considerable mortality occurs in this life stage. Parasitized nests had on average 5.9 full-grown *M. alcon* caterpillars (Thomas & Elmes 1998).

From the previous evidence we predict that (i) host plants with a higher adoption chance (i.e. one or more host-ant nests nearby) are preferred for oviposition early in the flight season; and (ii) the number of eggs increases more strongly on host plants with a low(er) adoption chance in the course of the flight season. We tested these predictions with repeated egg count data from a Belgian and a Dutch population of *M. alcon*.

2. METHODS

(a) *The study species*

Throughout Europe, *M. alcon* has a scattered distribution (Wynhoff 1998). In Belgium and The Netherlands, it is a threatened species living in wet *Erica* heathlands with the Marsh gentian (*Gentiana pneumonanthe*) as its unique host plant (Maes & Van Dyck 1999). This perennial plant is also rare, and in need of active conservation (Oostermeijer *et al.* 1994, 1998). In this part of its distribution, *M. alcon* is mainly specific to the host ant *Myrmica ruginodis* (Elmes *et al.* 1994; Scheper *et al.* 1995; J. G. B. Oostermeijer, I. Wynhoff and H. van Dyck, personal observations), but elsewhere other *Myrmica* species can operate as the regional or local optimal host (Elmes *et al.* 1994). Compared to other *Myrmica* species, *Myrmica ruginodis* typically occupies the relatively cold and wet microsites (Elmes *et al.* 1998), but mostly several *Myrmica* species co-occur. Larvae of *M. alcon* are adopted by any *Myrmica* species, but the survival in non-host nests appears to be extremely low (Thomas *et al.* 1989). Adults are on the wing in July–August for about four to five weeks, but individual longevity is on average less than one week.

(b) *The study areas*

Two independent data sets on oviposition patterns were used. The first was collected during 1997 in Liereman nature reserve in Oud-Turnhout (North Belgium; 51° 20′ N, 5° 05′ E). This study area consisted of a mosaic of wet heathland patches with *Erica tetralix*, surrounded by dry heathland with *Calluna vulgaris* and a scattered presence of small pines and birches, and a more homogeneous wet heathland with *Sphagnum*, lower densities of *Erica* and dominant *Molinia caerulea*. The second data set was collected during 1998 in an area within the Hoge Veluwe National Park in The Netherlands, called 'Deelense veld' (52° 10′ N, 5° 50′ E), which consisted of a wet heathland with *Erica tetralix*, *Molinia caerulea*, *Rhynchospora alba*, *Rhynchospora fusca* and *Trichophorum cespitosum*.

(c) *Egg counts and survey of ants*

The number of eggs per gentian was repeatedly counted during the butterfly's flight period, whereas the presence of *Myrmica* nests around each gentian was examined once. The white eggs on the outside of the gentian buds, are very conspicuous and easy to count in the field by visual inspection. After basal hatching, eggs remain for several days to weeks on the host plant (Thomas *et al.* 1991). Searching for *Myrmica* nests requires some disturbance of the vegetation since poorly visible sites (e.g. old grass tussocks) need to be 'opened' by means of a small knife. Workers of each nest were collected and identified to the species level (Wardlaw *et al.* 1998). At the Liereman, ant nests were searched within a radius of 3 m around each gentian, representing the foraging distance of *Myrmica* worker ants (Elmes *et al.* 1998), and hence the area in which caterpillars have a high adoption probability. At the Hoge Veluwe, all gentians, eggs and ants were mapped within four study plots of different size (140–300 m^2). From these data we extracted a subset which could be used in a similar way to the data set of Liereman. Hence, gentians within the 3 m border zone of the study plots had to be excluded from the analysis. In the final data set, 85 adult gentians were included for the Liereman, and 115 (in four plots) for the Hoge Veluwe. The presence or abundance of ant nests per gentian was divided into three classes: no nest, one nest, or more than one (two, seldomly three) nest of *M. ruginodis*, and similarly for the other *Myrmica* species (pooled for the present analysis). In Liereman only four gentians had more than one nest for either *M. ruginodis* or for the other species pooled. Therefore, the classes with one and more nests were grouped together. For the Hoge Veluwe all three classes were used.

Since taller gentians (measured as maximum height of the plant) had on average more flower buds ($r = 0.44$, $n = 80$, $p < 0.0001$), and hence more oviposition space available, we used the ratio of the number of eggs to the number of buds as a measure of egg load per gentian. Although at Liereman the butterfly occurred in two types of wet heathland, we did not use habitat as a factor in the analysis since (i) mark–release–recapture data showed exchange between all sites, and particular individuals were observed ovipositing in both types; (ii) the apparency of the gentians, and hence the available space per gentian for laying eggs, did not differ between the habitats with respect to gentian height (mosaic heath: 26.3 ± 0.9 cm; *Sphagnum* heath: 27.9 ± 1.8 cm; ANOVA: $F_{1,79} = 0.59$, $p > 0.44$) or number of flower buds (mosaic heath: 3.6 ± 0.3; *Sphagnum* heath: 3.4 ± 0.3; ANOVA: $F_{1,86} = 0.23$, $p > 0.63$); and (iii) variation between the habitats is probably not independent of variation in the occurrence of ants, and the latter factor, which is of main interest to our study, was incorporated in the analysis.

(d) *Statistical analyses*

The relationship between egg load and the presence of *M. ruginodis* and other *Myrmica* nests was analysed for both study areas separately by log-linear mixed regression models with a Poisson error structure (SAS package: Glimmix-macro; Littell *et al.* 1996) at the beginning (i.e. after one week) and the end of the flight season. This was done in a multivariate model, incorporating both ant groups simultaneously. Since data for Hoge Veluwe were collected within four study plots, plot was included into the analysis as a random factor. This requires a mixed model approach (Littell *et al.* 1996) with number of *M. ruginodis*

Table 1. *Log-linear mixed regression models for the relationship of the egg load per gentian of* Maculinea alcon *butterflies in relation to the number of* M. ruginodis *nests and of other* Myrmica *nests nearby*

	numerator degrees of freedom	denominator degrees of freedom	*F* (type III)	*p*
at the beginning of the flight season				
Liereman				
M. ruginodis	1	82	5.24	0.024
not *M. ruginodis*	1	82	0.23	0.63
Hoge Veluwe				
M. ruginodis	2	107.53	4.11	0.019
not *M. ruginodis*	2	108.88	2.45	0.091
at the end of the flight season				
Liereman				
M. ruginodis	1	82	5.45	0.022
not *M. ruginodis*	1	82	2.63	0.108
Hoge Veluwe				
M. ruginodis	2	109.05	2.82	0.064
not *M. ruginodis*	2	108.27	2.99	0.054

and 'not *M. ruginodis*' ant nests in the vicinity of the individual host plant as fixed effects. For the Liereman, only these fixed effects were involved.

To test the prediction of a temporal shift (i.e. a stronger increase in egg load during the season for gentians with fewer nests nearby), a log-linear mixed regression model for egg load per gentian was constructed with date of count, number of *M. ruginodis* nests, number of not *M. ruginodis* nests and each of the two two-way interaction terms with date as fixed effects. A significant date–*M. ruginodis* interaction, with higher parameter estimate values when less or no *M. ruginodis* nests are present (i.e. a higher increase in egg load for gentians with fewer *M. ruginodis* nests) is required to support our prediction. Because eggs were repeatedly counted on the same individual plants, data were not statistically independent. Therefore, the temporal change of egg load at the individual level was modelled in a random effects structure, hereby imposing a random intercept and slope. Denominator degrees of freedom of *F*-tests of the fixed effects were approximated with Satterthwaite's procedure (Verbeke & Molenberghs 1997). For Hoge Veluwe, study plot was also treated as a random effect in the model (besides individual gentian). Obviously, for the analysis of the temporal shift only gentians that received at least one egg were included.

3. RESULTS

Early in the flight season, gentians within foraging range of one or more nests of *M. ruginodis* had significantly more *M. alcon* eggs than gentians without nests at both study sites. Such a relationship was lacking when considering the other *Myrmica*s (table 1 and figure 1). Late in the flight season, gentians in the Liereman site surrounded by one or more nests of *M. ruginodis* still had higher egg loads, and again for the other *Myrmica* species there was no significant relationship (table 1 and figure 1). For the Hoge Veluwe site, however, there was no longer a significant relationship between final egg load and the occurrence of *M. ruginodis*, and the trend was even weaker than the (also non-significant) relationship with the other *Myrmica* group.

Next we tested for a temporal shift in host-plant choice towards gentians with lower adoption chance (table 2). For both study sites, the temporal increase in egg load was indeed higher for gentians with no *M. ruginodis* nests than for those with one or more nests—expressed by the significant interaction term *M. ruginodis* × date (figure 2). Overall, the latter plants received significantly more eggs. The presence of not *M. ruginodis* nests did not affect egg load, nor the temporal change.

4. DISCUSSION

Although oviposition in obligate myrmecophilous *Maculinea* butterflies has been considered to be random in relation to host ants (Thomas *et al.* 1989; Fiedler 1991; Hochberg *et al.* 1994), our results suggest that the presence of host ants does play a role, although not necessarily a direct one, in *M. alcon*. At both study sites, gentians surrounded by one or more nests of the optimal host ant received significantly more eggs than those outside the ants' foraging range. However, it is not a case of 'simple' ant-dependent oviposition either, since progressively more eggs are laid on gentians with no host ants in their vicinity towards the end of the flight season. The explicit test of a temporal shift in oviposition preference supported the predicted density-dependent shift in oviposition preference. For the study area Hoge Veluwe, the relationship between final egg load and host ants was absent, although there was a significant relationship early in the flight season. Hence, the absence of a correlation when counting eggs only once at the end of the flight period should be interpreted carefully.

Our results do not necessarily imply that *M. alcon* can detect host ants directly (i.e. by visual or olfactory cues), as has been observed in specific ant-tended lycaenids (Atsatt 1981; Pierce & Elgar 1985). Unlike many ants, *Myrmica* species—which mainly forage on the ground and hence not specifically on the gentians—reportedly have short-lived pheromone foraging trails which makes direct detection by the butterfly difficult. Moreover, the peak timing of oviposition by *M. alcon* does not coincide

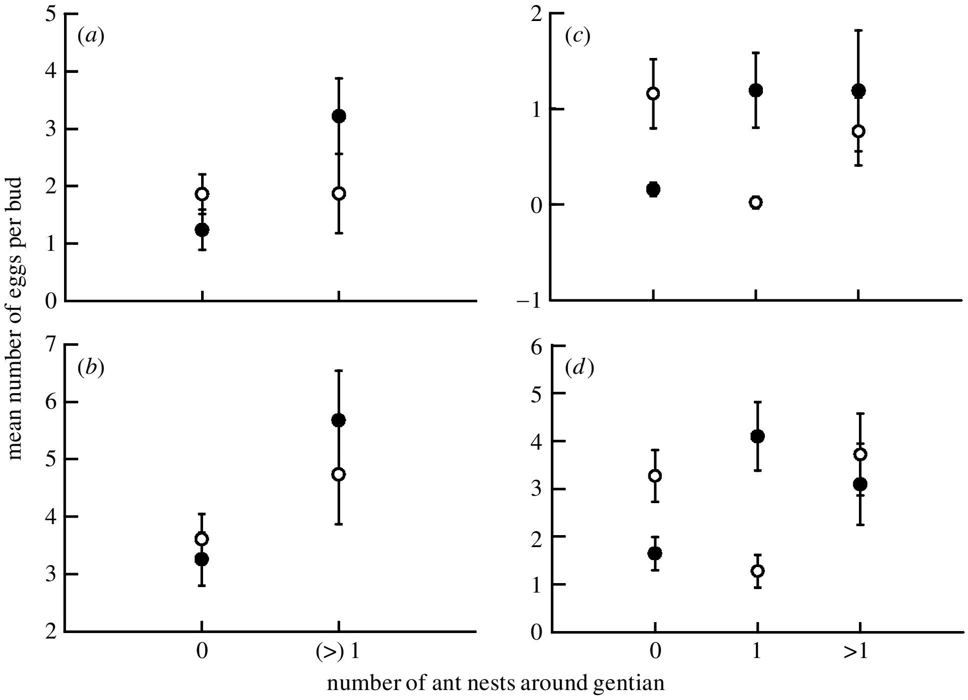

Figure 1. Relationship between mean egg load per gentian (± s.e.) and the presence of nests of the host ant *M. ruginodis*, and of other *Myrmica* ants. Study area Liereman (*a*) at the beginning and (*b*) the end of the flight season; study area Hoge Veluwe (*c*) at the beginning and (*d*) the end of the flight season. Solid symbols, *M. ruginodis*; open symbols, other *Myrmica* ants.

Table 2. *Log-linear mixed regression models for the relation of the egg load per gentian in relation to date, number of ant nests and their interaction terms for both study areas*

(Individual gentian was treated as a random effect in the model. In the case of the Hoge Veluwe site, this was also the case for study plot (cf. §2(d)).)

	numerator degrees of freedom	denominator degrees of freedom	*F* (type III)	*p*
Liereman				
date	1	77.83	68.94	0.0001
M. ruginodis	1	84.94	12.60	0.0006
not *M. ruginodis*	1	100.33	0.08	0.7788
date × *M. ruginodis*	1	85.11	9.91	0.0023
date × not *M. ruginodis*	1	98.36	3.34	0.0707
Hoge Veluwe				
date	1	2.722	9.45	0.0618
M. ruginodis	2	130.278	6.80	0.0016
not *M. ruginodis*	2	201.45	1.73	0.1800
date × *M. ruginodis*	2	97.670	3.74	0.0271
date × not *M. ruginodis*	2	11.808	1.15	0.3499

with the peak foraging activity of *M. ruginodis* workers which often avoid the hot sunny conditions between roughly 11.00 and 16.00 in such heathlands. Besides spotting and following foraging workers or their trails, which does not seem to be an available option, females may locate ant nests prior to a series of oviposition events. However, whether they are capable of doing so is not known. We did observe some females lingering for several minutes within a vegetation patch known to be without gentians, typically fluttering at low height. Nevertheless, we cannot exclude that indirect mechanisms are used to locate or predict the presence of host-ant nests via detecting relevant parameters of microclimate and vegetation structure. Clearly our results demand for further research including detailed behavioural studies on oviposition.

Our prediction for a counterbalancing influence of current egg load on oviposition was based on the assumption that gentians carrying several eggs provide some kind of signal that depresses oviposition motivation. Although there is no direct evidence on the mechanism in *M. alcon*, the recognition and rejection of host plants with many conspecific eggs has been shown in several Lepidoptera and other insects (Jones 1991; Dempster 1992). At

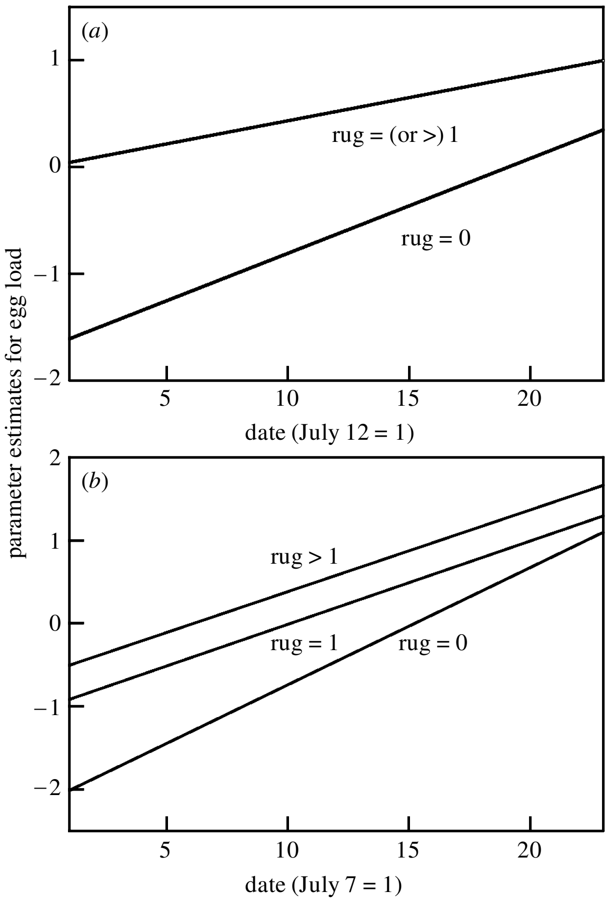

Figure 2. Temporal pattern in egg load of individual gentians in relation to the presence of the host ant *M. ruginodis*. Lines are based on the calculated regression lines (using the parameter estimates) from the log-linear mixed regression model analysis for (*a*) Liereman (slopes of the regression lines for rug = (or >) 1 and for rug = 0 differ significantly, $p = 0.001$), and (*b*) Hoge Veluwe (slope of the regression line for rug = 0 differs significantly from rug = 1 and rug > 1 ($p = 0.02$), which do not differ significantly from one another). 'Rug' refers to the classes of gentians with no (rug = 0), one (rug = 1) or more than one (rug > 1) nest of *M. ruginodis*.

least to the human eye, the white eggs are readily visible on the gentian buds, but the influence of other cues (e.g. olfactory cues like deterrency pheromones) cannot be ruled out.

But what about the influence of particular traits of the host plant and/or microhabitat on oviposition? Factors such as nutritional value interacting with flowering phenology may be of additional importance and may even provide alternative, causal explanations for the observed relationships. For instance, different gentians may become suitable for oviposition at different times during the flight period, depending on microclimate. This would lead to a succession of plants suitable for oviposition coinciding with first one and then another species of *Myrmica* as they have different microclimatic preferences. However, this scenario is not very likely since, at least in north-west Europe, individual marsh gentians do not have such restricted time-windows for oviposition, since flower development is not synchronized among buds of a single gentian (J. G. B. Oostermeijer, personal observations). In other words, there is no evidence that variation in availability for oviposition over time within an individual gentian is always smaller than among gentians. This probably deviates from the situation in the closely related *M. rebeli* using *Gentiana cruciata* on calcareous grasslands. Furthermore, the egg load still increased on gentians that were heavily laid on early in the season, albeit at a slow rate. Finally, although it was not quantified in this study, we observed females using buds of different age (including flowers) for oviposition.

In our opinion, it is safe to conclude that host-ant nests (either directly or indirectly) influence oviposition in *M. alcon*, but nevertheless traits of gentians and of the vegetation are important enough to be included in our further research, to evaluate their role relative to those of the ants. Interestingly, recent data on *M. nausithous* and *M. teleius* (I. Wynhoff, M. G. A. van der Heijden, J. G. van der Made, S. Plat, H. H. T. Prins, M. van Steells and M. Woyciechowski, unpublished data) support our view that the trade-off hypothesis is not exclusively applicable to *M. alcon*.

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