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Does enemy-free space for eggs contribute to a leaf beetle's oviposition preference for a nutritionally inferior host

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Summary

1. Natural enemies are likely to influence the interactions between herbivorous insects and their host plants. In particular, selection exerted by natural enemies could favour host-plant switches and cause, or maintain, oviposition preference for a host species that is nutritionally inferior to another acceptable host.

2. In a previous study, it was shown that larvae of the leaf beetle *Oreina elongata* perform better on *Adenostyles alliariae* (Asteraceae) than on *Cirsium spinosissimum* (Asteraceae). Moreover, *A. alliariae* provides larval and adult beetles with sequestrable chemical defences. However, in the field, egg densities are much higher on *C. spinosissimum* than on adjacent *A. alliariae*.

3. In this study, it was investigated whether this oviposition pattern could be maintained by *C. spinosissimum*, providing the eggs of *O. elongata* with better protection from natural enemies. In a field experiment, the survival of eggs was quantified on plants of each of the two species, with and without enemy exclusion.

4. Egg survival was equal for both host species when enemies were excluded from the plants, but it was higher on *C. spinosissimum* than on *A. alliariae* when enemies were allowed to the plants. It was also experimentally tested whether the higher egg densities observed in the field on *C. spinosissimum* are actually due to oviposition preference by the beetle. In a no-choice test, females laid more eggs on *C. spinosissimum* than on *A. alliariae*.

5. It can thus be confirmed that *C. spinosissimum* is really preferred for oviposition and it is concluded that this preference is likely to be maintained, at least partly, by a higher egg survival on *C. spinosissimum* due to enemy-free space provided by this host plant.

Key-words: Evolution of host range, preference–performance relationship

Introduction

The study of the evolution of host-plant range in herbivorous insects is mainly concerned with the mechanisms that restrict the number of plant species that insects can use, i.e. with the evolution of host specialization. Herbivorous insects should lay their eggs on host-plant species that provide the best conditions for egg or larval development and survival, especially if larvae are not mobile enough to switch between plants. If larval performance depended solely on the ingested plant chemicals, a positive correspondence should exist between the plant species preferred for oviposition and larval performance (Futuyma & Peterson 1985; Thompson 1988; Jaenike & Holt 1991). However, several examples are known of insects that preferentially oviposit on plants that provide suboptimal conditions for larval development (e.g. Atsatt 1981; Bernays & Graham 1988; Singer *et al*. 1988; Roininen & Tahvanainen 1989; Denno *et al*. 1990; Valladares & Lawton 1991; Rank 1994; Orians *et al*. 1997; Berdegué *et al*. 1998). Therefore, food quality alone does not provide a sufficiently general explanation for host specialization by herbivorous insects.

Ecological variables, such as natural enemies or plant phenology, may hinder the establishment of a positive relationship between oviposition preference and larval performance. Given that natural enemies can potentially affect the population dynamics and communities of

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insects (Gilbert & Singer 1975; Jeffries & Lawton 1984; Strong *et al.* 1984), it is not surprising that their role as selective forces acting on insect host-use has been the object of several studies (e.g. Atsatt 1981; Bernays 1989; Denno *et al.* 1990; Brown *et al.* 1995; Feder 1995; Berdegué *et al.* 1996; Björkman *et al.* 1997; Keese 1997; Rank *et al.* 1998; Gratton & Welter 1999; Yamaga & Ohgushi 1999). A plant species can be said to provide enemy-free space to an insect if it gives the insect a higher degree of protection against natural enemies than an alternative host plant (Jeffries & Lawton 1984). Often, enemy-free space seems to be mediated by some plant secondary chemical compounds that the feeding insects sequester and use as chemical defences (Price *et al.* 1980; Denno *et al.* 1990; Björkman *et al.* 1997; Keese 1997). For instance, the leaf beetle *Phratora vitellinae* strongly preferred to lay its eggs on a willow species that provided larvae with sequestrable defensive salicylates rather than on a salicylate-poor willow. Larvae raised on the salicylate-poor willow performed well in the absence of predators but suffered high mortality when predators were present (Denno *et al.* 1990). Chemically mediated enemy-free space may be common, since the sequestration of plant allelochemicals for chemical defence is widespread among the herbivorous insects (Rowell-Rahier & Pasteels 1992). However, morphological plant characters may also provide protection from natural enemies (Feder 1995; Abrahamson & Weis 1997; Larsson *et al.* 1997). An example is given by the host plants of the Apple Maggot Fly *Rhagoletis pomonella*. Fly larvae that are feeding inside apple fruits are better protected against parasitoids than larvae feeding inside hawthorn fruits because the larger size of apples allows larvae to escape from the reach of the short parasitoid ovipositor (Feder 1995).

Most investigations relating enemy-free space to insect host-selection have emphasized the insect larvae, but natural selection may also favour oviposition on plants that give enemy-free space to eggs. Eggs seem to have been investigated in only three out of 21 terrestrial insect systems cited in two previous reviews (Jeffries & Lawton 1984; Berdegué *et al.* 1996) and in only one out of six further studies (Brown *et al.* 1995; Feder 1995; Björkman *et al.* 1997; Keese 1997; Gratton & Welter 1999; Yamaga & Ohgushi 1999). In a recent investigation, the eggs of the leaf beetle *Ophraella notulata* had a higher survival on the normal host plant than on a novel host (Keese 1997). The chemical protection of the eggs did not influence that result (Keese 1997), suggesting that some feature of the host plants was responsible for the findings.

Here, we present a field study in which we tested whether natural enemies may explain why, in the field, eggs of the leaf beetle *Oreina elongata* Suffrian (Coleoptera: Chrysomelidae) occur in higher densities on a host plant that provides larvae with a lower food quality compared with a second host. In the population we studied, *O. elongata* oviposits preferentially on *Cirsium spinosissimum* (L.) (Asteraceae) in spite of the fact that, in the laboratory, larvae perform better on the other host *A. alliariae* (Gouan) (Asteraceae) (Ballabeni & Rahier 2000) and that *A. alliariae* also provides larvae with sequestrable pyrrolizidine alkaloids (PAs) as chemical defences (Dobler & Rowell-Rahier 1994; Dobler *et al.* 1996). Moreover, in the field, large numbers of larvae actually move from *C. spinosissimum* onto the adjacent *A. alliariae* during their development (Ballabeni *et al.* 2001). Previous results also indicated that *O. elongata* eggs survive better on *C. spinosissimum* than on *A. alliariae* (Ballabeni *et al.* 2001). These findings strongly suggest that, within the study population, the oviposition preference for *C. spinosissimum* does not benefit larvae, but it is rather maintained by natural selection acting on eggs. In this study we tested therefore the hypothesis that *C. spinosissimum* provides *O. elongata* eggs with a higher protection against natural enemies than *A. alliariae*.

We also show some experimental evidence of the beetle's oviposition preference for *C. spinosissimum*.

Materials and methods

STUDY ORGANISMS AND POPULATION

The study was conducted on the Petit Saint-Bernard Pass, which lies in the Western Alps, at the border between the regions of Savoie, France, and Vallée d'Aoste, Italy. The pass is located above the tree line at 2188 m elevation. *Adenostyles alliariae* and *C. spinosissimum* are present in patches of various sizes, which include either one or the other plant species or both. The area is characterized by severe winters and short summers. Adults of *O. elongata* start their reproductive season when the snow has almost completely melted, usually at the end of June but in some years not before mid-July. Eggs are laid through the month of July until the first half of August.

In the study population, *O. elongata* oviposits and feeds on both *A. alliariae* and *C. spinosissimum*. However, the mean number of eggs found on an individual plant of the latter species is 3–15 times higher than the number found on a plant of the first species. Furthermore, those *C. spinosissimum* that grow adjacently to *A. alliariae* are more likely to get eggs than the ones that grow more than 5 m away from the next *A. alliariae* (Ballabeni *et al.* 2001). It seems therefore that the beetle favours a close proximity of both plants.

As stated above, *A. alliariae* produces sequestrable PAs, whereas *C. spinosissimum* does not. *Oreina elongata* of populations that live in places where only the latter plant is present are able to rely on self-synthesized cardenolides for their defence (Dobler & Rowell-Rahier 1994). Unlike *A. alliariae*, *C. spinosissimum* has very spiny and hairy, dentate leaves that may give some degree of physical protection to *O. elongata* eggs or larvae.

EXPERIMENTAL PROCEDURE

To test whether eggs of *O. elongata* are better protected from natural enemies when they are laid on

Table 1. Number of replicates for each treatment, in the different plots and trials. One trial within plot C had to be dropped from the experiment (see text)

	Plot					
	H		C	R		
Treatment	Trial 1	Trial 2	Trial 3	Trial 4	Trial 5	Sum
Adenostyles alliariae						
Enemies allowed	6	5	5	6	5	27
Enemies excluded	6	5	5	6	6	28
Cirsium spinosissimum						
Enemies allowed	7	6	6	6	8	33
Enemies excluded	7	6	6	6	6	31

C. spinosissimum rather than on *A. alliariae*, the survival of eggs under natural conditions on both host-plant species was compared. The experiment was conducted under natural conditions, except that natural enemies were excluded from half of the plants of each species. The resulting four experimental treatments were replicated a number of times in three different plots within the study site. Two trials of the experiment were started in each plot to increase the number of replicates. Thus, we performed a factorial experiment, with plant species, enemy exclusion, plot and trial as independent factors and the counts of eggs, repeated over time, as the dependent variable. The numbers of replicates for each combination of plant species, enemy exclusion, plot and trial are given in Table 1. In total, 119 plants were the experimental units on which eggs were counted. The experiment was performed between 8 July and 15 August 1999.

The three plots on which the experiment was performed were two distinct plots that are colonized by *O. elongata* (plots H and C) and one plot (R) in which the host plants are naturally present but not colonized by the beetle. The experiment was given a spatial dimension to take into account potential differences in the enemy fauna between the plots, especially between the two colonized plots and the non-colonized one. Plots H and C were about 500 m apart and the area between them contained several uncolonized host-plant patches. Plot R was about 200 m from plot C and 700 m from plot H. Non-colonized host-plant patches were also present between plot R and the other two plots. The distances between plots were very unlikely to be covered by *O. elongata* within a reproductive season, since adults only walk and never fly. Indeed, this beetle shows an extreme host-patch fidelity. In a mark–recapture study, only three out of 50 adults left their host patch over a whole season: two of them were recaptured less than 2 m away from the original patch and one individual exceptionally walked 65 m away from its patch (D. Conconi, unpublished data).

Each trial was started on a different day and two trials within the same plot were performed adjacently to each other. For each trial, between 14 and 16 plants of each species were chosen, distributed in such a way as to avoid spatial segregation between species. To obtain eggs of the same age, two gravid, field-collected female *O. elongata* were caged on each experimental plant and allowed to lay eggs during 48 h, after which they were removed. Before caging the females, we made sure that the experimental plants did not bear any previously laid eggs. Plants were caged by fine-meshed nylon bags that were tightly closed around the plant stem by a string. The females were collected from both host-plant species and caged on the experimental plants on the same day. Each female was randomly assigned to its experimental plant. Beetles from plot H were used for the trials on plots H and R (the non-colonized plot), and beetles from plot C for the trials on plot C. After removing the females, the eggs that had been laid were counted and half of the plants of each species were caged to hinder natural enemies in reaching the eggs. The other half of the plants remained uncaged and natural enemies could freely access them. The plants on which no eggs were laid were excluded from the experiment, which is reflected by the differential replicate numbers reported in Table 1. A whole trial on plot C was also dropped because only two out of seven *A. alliariae* were oviposited on, resulting in a very unbalanced design. Eggs were counted on the day the ovipositing females were removed and again 7 and 14 days later. In this way it was possible to quantify egg survival over almost the whole egg development time, since eggs eclose 15–20 days after oviposition in the field. To avoid the risk of counting any egg that could have been laid by beetles coming later to the uncaged plants, the experimental eggs were marked with circles drawn around them on the plant leaves with a permanent marker.

This procedure also served as a no-choice experiment to test whether *C. spinosissimum* was preferred over *A. alliariae* for oviposition. To do this, the numbers of eggs laid on plants of either species over 48 h by the caged females were compared. No-choice experiments of this kind have been used to quantify oviposition preference in insects (e.g. Singer 1982; Singer *et al.* 1988; Ekbom & Borg 1996; Gratton & Welter 1998).

STATISTICAL ANALYSIS

Given that repeated egg counts on the same individual plants cannot be considered independent from each other, the data were analysed with a mixed-model factorial multivariate analysis of variance (MANOVA). A MANOVA procedure rather than a more powerful univariate repeated-measures analysis of variance (ANOVA) was preferred because repeated-measures ANOVA is based on a restrictive assumption about the variance–covariance matrix of the within-subject variable (the repeated measure), which it is not likely to be met in our data (von Ende 1993). On the contrary, MANOVA does not make any assumption about the variance–covariance matrix but it requires that the total number of measurements minus the number of between-subject levels be larger than the number of dependent variables (von Ende 1993). Since our data set consisted of 119 × 3 = 357 measurements, 2 (plant species) × 2 (enemy exclusion) × 5 (trials) = 20 between subject levels

Table 2. MANOVA for egg survival during the experiment. Survival was measured as the proportion of *O. elongata* eggs present on each plant

	Statistic	Value	*F*	Numerator df	Denominator df	*P*
Time	Pillai trace	0·746 333	4·8084	26	210	<0·0001
Trial × Time	Pillai trace	0·072 273	1·9683	4	210	0·1005
Plot × Time	*F*-test	0·049 188	2·5578	2	104	0·0823
Plant species × Time	*F*-test	0·035 252	1·8331	2	104	0·1650
Enemy exclusion × Time	*F*-test	1·075 767	55·9399	2	104	<0·0001
Plot × Plant species × Time	Pillai trace	0·040 851	1·0947	4	210	0·3602
Plot × Enemy exclusion × Time	Pillai trace	0·112 729	3·1359	4	210	0·0156
Plant Species × Enemy exclusion × Time	*F*-test	0·112 237	5·8363	2	104	0·0040
Plot × Plant species × Enemy exclusion × Time	Pillai trace	0·082 544	2·2601	4	210	0·0638

and 3 dependent variables (repeated egg counts), this requirement was clearly met and, additionally, our MANOVA should be powerful (see discussion in von Ende 1993).

Trial was considered to be a random factor since we were not interested in the differences among trials but wanted to control for their variation. In contrast, plot, plant species and enemy exclusion were the independent variables of interest and were therefore analysed as fixed factors. The dependent variables were the proportions of eggs surviving on the plants at each count. Proportions were transformed by the arcsin of their square root before analysis, to meet the ANOVA assumption of homogeneity of variances (Sokal & Rohlf 1995). Since we were interested in the changes of the egg numbers over time, only the interactions between the independent factors and time were analysed, not the main factors alone. Particularly, if *C. spinosissimum* provides *O. elongata* eggs with a higher degree of protection against natural enemies, this would be shown by a statistical interaction among the effects of host-plant species, protection from the enemies and time.

The profile analysis procedure in the multivariate platform of the statistical package JMP (SAS 1989) was run. As test statistics either the exact *F* or the Pillai trace with its approximate *F* is given, as appropriate (SAS 1989). The Pillai trace was chosen rather than other available multivariate test statistics because the *P*-values of the Pillai traces tended to be slightly more conservative in our analysis.

To test the oviposition preference for *C. spinosissimum*, an ANOVA was run on the transformed number of eggs laid on each plant. A higher oviposition on *C. spinosissimum* would show a preference for this plant, since beetles were left for the same amount of time on plants of either species (Ekbom & Borg 1996). In this analysis, trial was a random factor, plot and plant species were fixed factors and egg number the dependent variable. Type III sums of squares were computed for the *F*-tests. The software JMP (SAS 1989) was used for the ANOVA as well.

Results

EGG SURVIVAL

A significant interaction between host-plant species, exclusion of natural enemies and time was found (Table 2). This interaction was caused by the egg survival rates being equal between plant species when enemies were excluded, but higher on *C. spinosissimum* than on *A. alliariae* when enemies were allowed to reach the plants (Fig. 1). Also, for both plant species, the exclusion of natural enemies resulted in higher egg survival rates than the non-exclusion (Fig. 1). This is also reflected by the significant enemy exclusion–time interaction (Table 2). A quantification of these results gave killing powers over 14 days (i.e. $-\log_{10}$ of the proportion surviving at the end of the experiment, the *k*-value of a life-table; Begon *et al.* 1996) of 0·1107 for *A. alliariae* with enemies excluded, 0·4698 for *A. alliariae* with enemies allowed, 0·0915 for *C. spinosissimum* with enemies excluded and 0·2907 for *C. spinosissimum* with enemies allowed. This means that natural enemies exerted a killing power of 0·3591 (i.e. 0·4698–0·1107) on eggs laid on *A. alliariae* and of 0·1992 (i.e. 0·2907–0·0915) on eggs laid on *C. spinosissimum*.

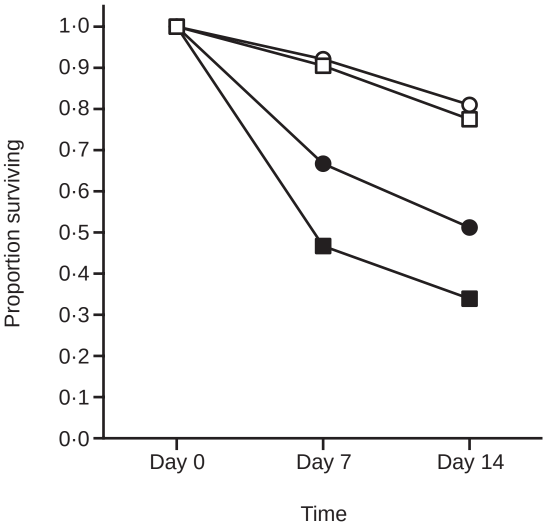

Fig. 1. The interaction between plant species, enemy exclusion and time for egg survival. —□— = *A. alliariae*, enemies excluded; —○— = *C. spinosissimum*, enemies excluded; —■— = *A. alliariae*, enemies allowed; —●— = *C. spinosissimum*, enemies allowed.

A significant three-way interaction between plot, enemy exclusion and was also obtained, meaning that the exclusion of natural enemies from the experimental plants differently affected egg survival in the three

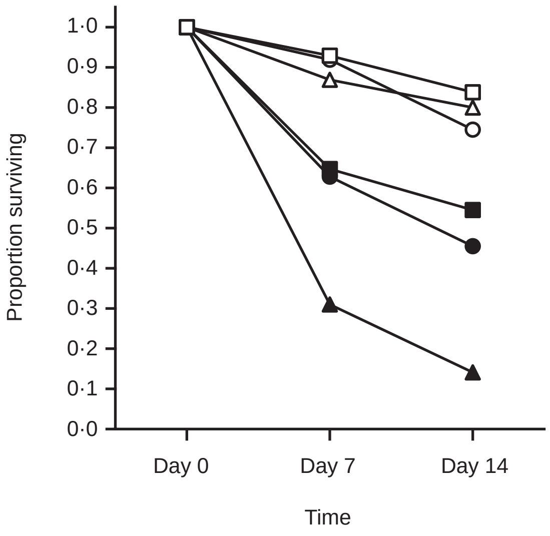

Fig. 2. The interaction between plot, enemy exclusion and time for egg survival. —□— = H, enemies excluded; —○— = R, enemies excluded; —△— = C, enemies excluded; —■— = H, enemies allowed; —●— = R, enemies allowed; —▲— = C, enemies allowed.

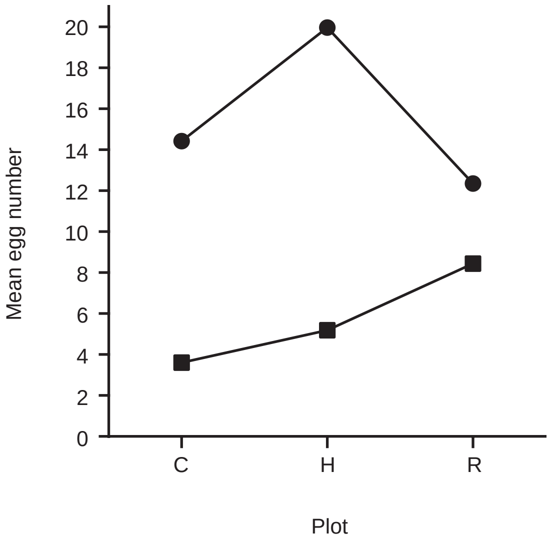

Fig. 3. The interaction between plot and plant species for the numbers of eggs laid per plant. —●— = *C. spinosissimum*; —■— = *A. alliariae*.

plots (Table 2). Eggs had similar survival rates among the three plots when natural enemies were excluded from the plants but mortality was much more dramatic in C than on the other two plots when enemies were allowed to reach the plants (Fig. 2). Furthermore, in H and R the survival patterns were strikingly similar, with a divergence between the two plots starting only after day 7 (Fig. 2). The killing powers for the eggs laid on plants growing in H were of 0·0786, with enemies excluded, and 0·2636 with enemies allowed. The figures were 0·1278, respectively, 0·3516 for R and 0·0969, respectively, 0·8508 for C. Thus, natural enemies exerted a killing power of 0·1868 in H (i.e. 0·2636–0·0768), of 0·2238 in R and of 0·7539 in C. No other factor or interaction had any significant effects on egg survival (Table 2).

OVIPOSITION PREFERENCE

The statistical interaction between plot and plant species was significant, indicating that the difference between the two plants in the beetle's oviposition activity was not consistent among the three plots (Table 3). However, the interaction diagram shows that in all three plots more eggs were laid on *C. spinosissimum* than on *A. alliariae* (Fig. 3).

Table 3. ANOVA for the numbers of eggs laid on 55 *A. alliariae* and 64 *C. spinosissimum*

Source of variation	df	*MS*	*F*	*P*
Trial	1	2·499 03	3·5902	0·0607
Plot	2	0·557 72	0·8012	0·4513
Plant species	1	58·659 93	84·2739	<0·0001
Plot × Plant species	2	5·807 50	8·3434	0·0004
Error	112	0·696 06		

Discussion

In the presence of natural enemies, the eggs of *O. elongata* had higher survival rates when laid on plants of *C. spinosissimum* than on *A. alliariae*, whereas egg survival did not differ between the two plants when enemies were excluded. This suggests that *C. spinosissimum* gives some enemy-free space to the eggs of *O. elongata*. Furthermore, *C. spinosissimum* was also the host species that was preferred for oviposition, in spite of the fact that this plant had been previously shown to provide larvae of *O. elongata* with food of a lower quality than *A. alliariae* (Ballabeni & Rahier 2000). Thus, the oviposition preference is likely to be at least partly maintained by selection favouring escape to enemy-free space in the Petit Saint-Bernard population.

Since natural enemies are often thought to exert a major impact on the survival of herbivorous insects, they may potentially play a major role in shaping the evolutionary trajectories of insect–plant relationships and particularly the evolution of host range (Gilbert & Singer 1975; Price *et al.* 1980). Natural selection may promote shifts onto new host plants that provide escape to enemy-free space (Price *et al.* 1980; Jeffries & Lawton 1984; Brown *et al.* 1995; Feder 1995; Gratton & Welter 1999). A shift to a new host may in turn favour the formation of host races within insect species and might ultimately favour speciation (Price *et al.* 1980; Diehl & Bush 1989). In the population we studied, enemy-free space provided by *C. spinosissimum* to the eggs of *O. elongata*, alone or in combination with some other factors, is likely to prevent the evolution of specialization on *A. alliariae*, which provides better developmental conditions and chemical defences to the beetle.

If *C. spinosissimum* gives eggs of *O. elongata* some protection from natural enemies, it is less likely that this plant does the same for larvae. Previous studies have shown that eggs are laid in higher densities on *C. spinosissimum* plants that grow adjacently to *A. alliariae* than on *C. spinosissimum* growing a few metres away from the other host (Ballabeni *et al*. 2001). Large numbers of larvae move then from *C. spinosissimum* to adjacent *A. alliariae* during their development (Ballabeni *et al*. 2001). Since the leaves of the latter plant contain sequestrable PAs, it is likely that for the growing larvae *A. alliariae* would give a better protection against enemies than the other host. We therefore hypothesize that in our study system each host plant possibly provides some degree of enemy-free space to a different developmental stage of *O. elongata*. However, we lack data about the natural enemies of larvae to test this idea.

Previous results suggest that, in addition to natural enemies, adverse weather conditions could also influence higher egg survival on *C. spinosissimum* compared with *A. alliariae* (Ballabeni *et al*. 2001). An egg survival experiment similar to the one of the present study but with the difference that no plant was protected from the natural enemies was conducted. In both trials of that experiment, a steep drop in the number of the eggs surviving on *A. alliariae* occurred on the same day, which had stormy weather and heavy rain. No such drop occurred to eggs laid on *C. spinosissimum*. Thus, the latter plant species may not only give the eggs increased protection against natural enemies but also a better substrate for egg adhesion. Indeed, *O. elongata*'s eggs are anchored among the hairy structures of the leaves and stems of *C. spinosissimum*, whereas no such structures are present on *A. alliariae* where the eggs depend only on being glued for adhesion. Since in the present study cages might have protected the plants against meteorological adversities as well as natural enemies, we cannot completely exclude that the meteorology influenced our results. However, the weather conditions were never extreme during the present experiment.

In spite of our limited knowledge of the potential natural enemies of *O. elongata* at the Petit Saint-Bernard we know at least one likely candidate as a predator of the beetle's eggs laid on *A. alliariae*. *Nebria gyllenhali* (Coleoptera: Carabidae) ate *O. elongata* eggs in a laboratory test (Jeanbourquin 1999) and has been observed climbing on *A. alliariae* on our field site (D. Conconi, personal communication). Three other carabid species, captured on the ground in *A. alliariae* and *C. spinosissimum* patches, have been tested positively for egg feeding in the laboratory, but we do not know whether they are able to climb onto plants (Jeanbourquin 1999). The differences in the effect of enemies we found between plots (Fig. 2) may be due to quantitative or qualitative differences in the enemy faunas between plots.

In conclusion, this and previous studies suggest an evolutionary scenario in which different developmental stages of *O. elongata* have highest fitness on different host plants. Eggs have higher survival on *C. spinosissimum*, whereas larvae grow faster and find sequestrable defensive compounds on *A. alliariae*. This may explain why egg densities are highest on those *C. spinosissimum* plants that grow adjacently to *A. alliariae* in the Petit Saint-Bernard population (Ballabeni *et al*. 2001). Thus, host-selection strategies of herbivorous insects may be shaped by between-plant trade-offs in the performance of individuals.

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