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# Response of a leaf beetle to two food plants, only one of which provides a sequestrable defensive chemical

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**Abstract** *Oreina elongata* is a chemically defended leaf beetle. If its food plant contains pyrrolizidine alkaloids, all life stages of the beetle sequester them. However, one of the two known host-plant genera does not contain these alkaloids. In this paper we compare the adult feeding preference and larval performance of two populations, one feeding on *Adenostyles alliariae* (which contains alkaloids) and one on *Cirsium spinosissimum* (devoid of alkaloids). Adults of the population living on *C. spinosissimum* preferred the alkaloid-containing *A. alliariae*, while adults of the population feeding on *A. alliariae* showed no preference for either plant. On the other hand, larval growth of both populations is better on *C. spinosissimum*, without alkaloids. This is especially so in the population that never naturally encounters pyrrolizidine alkaloids; the population living on *A. alliariae* is apparently better adapted to its host's secondary compounds. The data are discussed in terms of cost of defense and trade-offs between growth and defense.

**Key words** *Oreina elongata* · Larval performance
Cost of sequestration · Host plant adaptation
Pyrrolizidine alkaloids

## Introduction

Herbivorous insects are often restricted to a limited set of host plants. As Bernays and Graham (1988) pointed out, one of the advantages of such specialization may be better protection against generalist predators due to chemicals derived from the host plant. Specialization on toxic plants may, however, impose costs on the herbivore. First, the insect has to be able to tolerate these toxins and may suffer a metabolic load, i.e., a measurable diversion of energy from growth or fecundity to detoxification (see Cresswell et al. 1992) or, via lower assimilation rates, a reduction in size and fitness (e.g., Schoonhoven and Meerman 1978; Scriber 1981; Lindroth et al. 1986; Appel and Martin 1992). Sequestration of host plant toxins additionally requires transport and storage that may involve costs in terms of energy expenditure (reviewed in Bowers 1992; Rowell-Rahier and Pasteels 1992). Additionally, the plants providing the sequestrable toxins might not be optimal as food.

Leaf beetles are well known for their diverse chemical defenses (Pasteels 1993). In the adults the release of toxic secretions from specialised glands on the pronotum and elytra is commonly observed. Within the genus *Oreina* (Chevrolat) these secretions contain either cardenolides, produced *de novo*, or pyrrolizidine alkaloids sequestered from the host plant (Pasteels et al. 1989, 1992). Both compounds are known to be toxic and deterrent to vertebrates and invertebrates (e.g. Boppré 1986; Malcolm 1991), and have been shown to effectively protect the beetles against avian predators (M. Rowell-Rahier et al. 1994).

In this paper we use the leaf beetle *Oreina elongata* Suffrian and its host plants to investigate the costs of living on plants containing allelochemicals that can be sequestered. *O. elongata* is specialized on two asteraceous plant genera, *Adenostyles*, which contains pyrrolizidine alkaloids, and *Cirsium*, which does not. On *Adenostyles*, both adults and larvae of *O. elongata* sequester the alkaloids in the body and, in the case of the adults, in their defensive secretion (Dobler and Rowell-Rahier 1994, J.M. Pasteels et al. unpubl.). Most likely this provides all stages with a defense against predators. Some populations of *O. elongata*, however, feed exclusively on *Cirsium*, which does not afford this putative defense. On this plant the beetles and larvae have to rely on small amounts of autogenously produced cardenolides that probably do not suffice to protect the insects (Dobler and Rowell-Rahier in press; J.M. Pasteels et al. unpubl.).

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Comparing two populations, each restricted in the field to only one of the two potential host plants, we estimated their performance on each of them. To do this we measured the food preference of adults and the growth and survival of larvae on both plants, using individuals drawn from both populations. By comparing larvae fed on single food-plants with larvae which were transferred from their field host to the host plant of the other population, we also tried to assess whether local adaptation to the host plants and conditioning during the lifetime of the individual played a role in determining larval performance.

## Materials and methods

### Field sites and organisms

About 60 males plus females of *Oreina elongata* Suffrian (Coleoptera, Chrysomelidae, Chrysomelinae) were collected in July 1991 and 1992 at the Mattmark dam (Swiss Valais above Saas Almagell, 2000–2400 m altitude) and at the Col du Lautaret (French Alps near Briançon, Pied du Col, 2000 m altitude). The Mattmark population lives exclusively on *Cirsium spinosissimum* Scopoli, while the Col du Lautaret population feeds on two species of *Adenostyles*, mainly *A. alliariae* Kerner and to a lesser extent on *A. glabra* De Candolle. No *Adenostyles* was found in the vicinity of the population feeding on *C. spinosissimum* or vice versa.

The plants used in the experiments were collected every 3rd–4th day (*A. alliariae*) or every 6th–7th day (*C. spinosissimum*), and were kept in the refrigerator until used. *A. alliariae* was collected in the Swiss Jura mountains (at 900 m altitude on the Blauen above Hofstetten, Solothurn, Switzerland). *C. spinosissimum* was collected at 2000 m altitude at the Mattmark dam.

### Food choice experiment

Fifteen females of each population were put individually in plastic containers lined with a thin layer of moist plaster to prevent wilting of the food plants. Each female was presented simultaneously with six leaf disks of 1.5 cm diameter, three of *Adenostyles alliariae* and three of *Cirsium spinosissimum.* Both plants were freshly collected from the field on the day of the experiment. After 24 h the leaf disks were removed, scanned, their areas digitized with a computer and the area consumed calculated by subtraction. Additionally the average fresh weight of consumed leaf material was calculated, using the average weight of 20 additional freshly cut leaf disks of each tested plant species as a control.

### Larval performance

Larval growth and survival on *Adenostyles alliariae* and on *Cirsium spinosissimum* were measured in three separate experiments. During the experiments, all larvae were kept individually in petri dishes lined with a layer of moist plaster and a filter paper to obtain saturated humidity and were inspected daily.

#### *Constant diet experiments*

The eggs of 15 females of each population were collected, and the emerging larvae equally distributed between both food plants. There was no significant difference in mean initial weight between the two groups of either population. Shortly before the third (and last) molt 20 larvae of each of the four groups were put individually in petri dishes. The larvae were weighed on the day of molting and again three days later.

In a second experiment, four larvae were randomly taken from the progeny of each of 10 females from each population and equally distributed between both potential food plants. The resulting four groups of 20 larvae were fed every 2nd day and inspected daily for molting and survival. They were weighed on days 1, 4, 7, and 10. Larvae that died due to causes not related to the experiment (such as drowning in water condensation or escaping from the petri dish) were excluded from subsequent calculations. Both of the above experiments were performed in an environmental chamber at 17° C.

#### *Changeover experiment*

Four larvae, randomly taken from each of ten females per population, were reared in sibling groups until the second molt on the natural host plant of the population. On the day of molting the larvae were put individually in petri dishes. Two larvae of each sibling group were fed with the food plant of the other population. For the next 10 days the larvae were fed and weighed daily and inspected for molting and survival. The experiment was carried out in an incubator set to 15 h at 20° C and 9 h at 10° C.

### Statistical analyses

The adults' choice of food was analysed by paired *t*-test comparing the consumption of the two plants for each female. In the constant-diet experiment the weight of the larvae on the day of the third molt and 3 days later were analyzed by a repeated-measures analysis of variance with food group as the treatment factor, larvae within food group as the between-subject factor, used as denominator for the effect of the food group, and age as the period factor which was tested against the residual error.

To achieve linearity and an even distribution of the residuals the larval weights from experiments 2 and 3 were logarithmically transformed. Linear regressions were calculated for the logarithmic data and compared by analysis of covariance for different slopes between food groups within each population.

The weights of fourth-instar larvae in experiments 1 and 3 were compared by three-way analysis of variance with the effects population, food group, experiment, and all possible interactions.

## Results

Adults of both populations significantly preferred *Adenostyles alliariae* over *Cirsium spinosissimum* (Fig. 1a). However, as the leaves of *C. spinosissimum* are thicker than those of *A. alliariae*, the area consumed overestimates the difference in leaf material eaten. In Fig. 1b the consumed leaf area is multiplied by the average weight of the leaf disks. This measure, on the other hand, underestimates the difference in consumed material as the beetles avoid the leaf veins which are more prominent and contribute more to the average weight of the leaf disks in *C. spinosissimum.* The actual difference in consumption lies between these two values. Paired *t*-tests comparing the consumption of the two plants for each female show a significant preference of the Mattmark population for *A. alliariae* ($t = 10.59$, $P \ll 0.01$ for leaf area and $t = 2.68$, $P = 0.02$ for leaf weight), although they do not encounter this plant in the field. For the Col du Lautaret population the two estimation methods yield different results and it is therefore not possible to decide whether they prefer one or the other

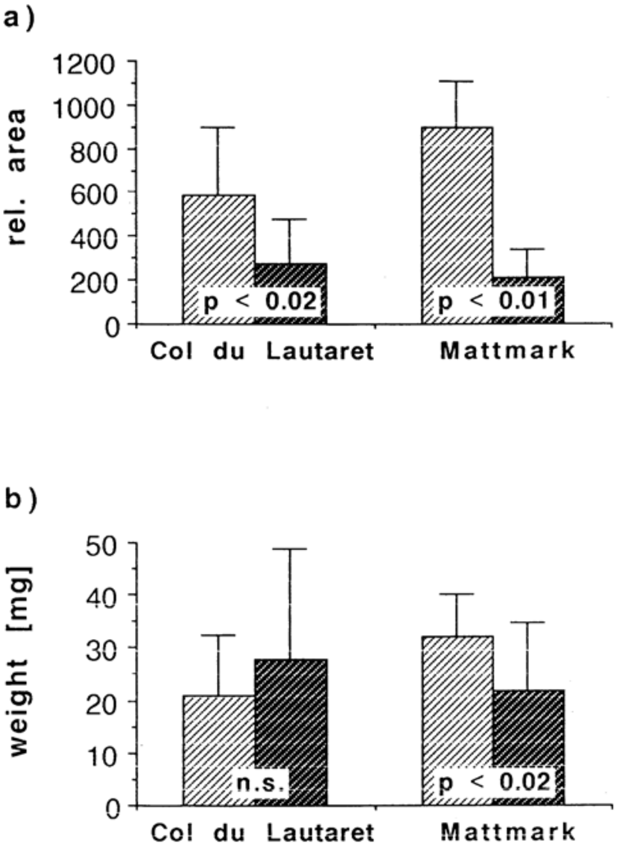

**Fig. 1a, b** Food choice of adults of *Oreina elongata* from the two populations: **a** area of the leaf disks consumed, **b** weight consumed. The *bars* indicate the standard deviation, the *P* values the statistical significance of the difference in a paired *t*-test. *Lightly shaded bars*, feeding on *Adenostyles alliariae*; *darkly shaded bars*, feeding on *Cirsium spinosissimum*

**Table 2** Repeated-measures analysis of variance of larval weight measured at the day of the third molt and again three days later (see Table 1a) (*df* degrees of freedom, *MS* mean square, *F*-value test statistic with *F*-distribution, *P* corresponding statistical significance)

| Source | *df* | MS | *F*-value | *P* |
|---|---|---|---|---|
| *Mattmark* | | | | |
| Food | 1 | 1014.9 | 47.1155 | 0.000 |
| Larva[food] | 37 | 21.541 | | |
| Age | 1 | 3763.9 | 404.7191 | 0.000 |
| Age × food | 1 | 120.55 | 12.9628 | 0.001 |
| *Col du Lautaret* | | | | |
| Food | 1 | 467.53 | 17.451 | 0.000 |
| Larva[food] | 36 | 26.791 | | |
| Age | 1 | 7087.0 | 348.316 | 0.000 |
| Age × food | 1 | 152.62 | 7.501 | 0.010 |

plant ($t=2.87$, $P=0.01$ for leaf area and $t=1.12$, $P=0.28$ for leaf weight). Like the other population they also accepted the plant they do not encounter naturally, in this case *C. spinosissimum*.

In the constant-diet experiment fourth instar larvae of both populations were significantly heavier when fed on *C. spinosissimum* (Table 1a). The results of a repeated-measures analysis of variance on the weight at the third molting and 3 days later are given in Table 2. For both populations the effects of food and age are highly significant; additionally there is a significant interaction between food and age, indicating that over this 3-day period the larvae grew differently on the two plants, gaining more weight per unit time on *C. spinosissimum*. This effect is even more pronounced in the Mattmark population. The result shows that no matter on which plant the beetles live naturally, they grow better on *C. spinosissimum* (Table 1).

We then analyzed the differential response to the two plants by comparing the growth curves over 10 days of (a) larvae that had been distributed among the food plants immediately after hatching (constant-diet experiment) and (b) larvae that had been raised to the second molt on their natural host plant and then distributed among the two plants (changeover experiment). Linear regressions of logarithmically transformed larval weight against age were calculated (Fig. 2). The slopes of the regression lines of the two food groups within each population were compared by analysis of covariance. The results of the two experiments differed. In the constant-diet experiment, a clear trend for better growth on *C. spinosissimum* appears in the Mattmark population after the first 10 days (Fig. 2a, $F_{1,147}=2.86$, $P=0.09$ for different slopes in the analysis of covariance). For the Col du Lautaret population, on the other hand, no dif-

**Table 1** **a** Weight (means ± SE; *n*) of larvae at third molt and three days later when raised from hatching on the indicated plants (constant diet), **b** weight of larvae at third molt that were grown on their natural food plant until the second molt, after which the two groups marked with a superscript a changed food plants (changeover)

| | Mattmark | | Col du Lautaret | |
|---|---|---|---|---|
| | *Adenostyles*$^{a}$ | *Cirsium* | *Adenostyles* | *Cirsium*$^{a}$ |
| **a** *Constant diet* | | | | |
| Third molt (mg) | 14.81<br>(±0.53; 19) | 19.54<br>(±0.86; 20) | 18.66<br>(±0.85; 19) | 20.46<br>(±0.86; 20) |
| 3 days later (mg) | 26.22<br>(±1.13; 19) | 35.93<br>(±0.93; 20) | 35.14<br>(±0.89; 19) | 42.93<br>(±1.65; 19) |
| **b** *Changeover* | | | | |
| Third molt (mg) | 13.88<br>(±0.75; 16) | 18.64<br>(±0.91; 20) | 19.63<br>(±0.87; 18) | 20.82<br>(±0.96; 20) |

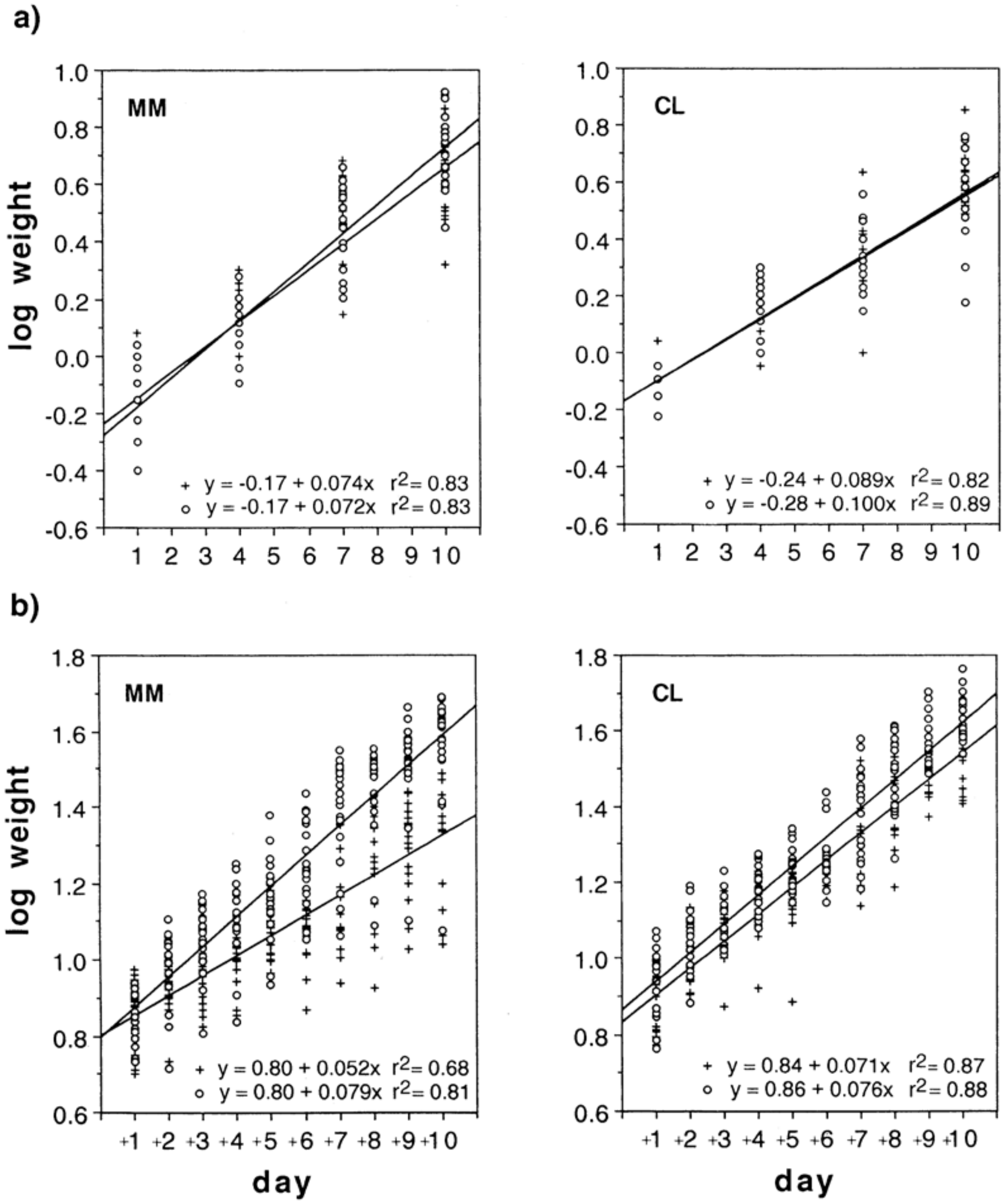

**Fig. 2a, b** Logarithmically transformed weight of larvae on *A. alliariae* (*crosses*) and *C. spinosissimum* (*circles*) **a** in the constant-diet experiment starting from hatching, **b** in the changeover experiment starting at the day of the second molt. For each food group the *equation* of a linear regression through the data is given. *MM* Mattmark population, *CL* Col du Lautaret population

ference in growth on the two plants can be detected after this time (Fig. 2a, $F_{1,139}=0.12$, $P=0.73$), although there is a significant difference at the time of the third molt (Table 2).

In contrast, the food plants had marked effects in the changeover experiment. The larvae from the *C. spinosissimum*-feeding Mattmark population that were transfered to *A. alliariae* after the second molting grew significantly worse than those that stayed on *C. spinosissimum* (Fig. 2b, $F_{1,376}=48.50$, $P \ll 0.01$ for different slopes). For the Col du Lautaret population the difference in growth on the two plants was similar, but less marked and just not significant (Fig. 2b, $F_{1,382}=3.48$, $P=0.06$). The weights of the larvae at the third molting (Table 1b) are similar to those of larvae on the same food plant in the constant diet experiment (cf. Table 1a, b: $F_{1,144}=0.04$, $P=0.87$ for the effect of experiment in a three-way analysis of variance with food and population as additional effects). Table 3 shows that there are no differences in instar duration and survival between the food groups within populations in the constant-diet experiment. Differences were found in the changeover experiment, however. Instar duration is significantly shorter and survival better for the Mattmark population on *C. spinosissimum* (*t*-test: Mattmark, $t=2.03$, $P<0.05$ for shorter instars, $\chi^2$ test: Mattmark, $\chi^2=8.49$, $P<0.01$, for better survival). No significant differences in either parameter were found for the Col du Lautaret population.

## Discussion

The data presented here suggests that *Oreina elongata* does less well on plants which contain the allelochemi-

**Table 3** Instar duration (means ± SE; *n*) and survival (% alive after 10 days and *n*) in **a** the constant-diet experiment and **b** the changeover experiment

| | Mattmark | | Col du Lautaret | |
|---|---|---|---|---|
| | *Adenostyles* | *Cirsium* | *Adenostyles* | *Cirsium* |
| **a** First-instar duration (days) | 6.37<br>(±0.31; 19) | 6.67<br>(±0.61; 18) | 7.67<br>(±0.26; 18) | 8.13<br>(±0.30; 16) |
| Survival | 95.0%<br>(20) | 94.4%<br>(18) | 89.5%<br>(19) | 88.9%<br>(18) |
| **b** Third-instar duration (days) | 6.88<br>(±0.26; 16) | 6.15<br>(±0.23; 20) | 6.94<br>(±0.15; 18) | 6.65<br>(±0.17; 20) |
| Survival | 65.0%<br>(20) | 100%<br>(20) | 90.0%<br>(20) | 100%<br>(20) |

cals that can be sequestered by the beetles. Of its two host plants, the one that contains pyrrolizidine alkaloids, *Adenostyles alliariae*, is also the one on which the larvae gain less weight. In insects the fecundity of females is generally assumed to correlate with the weights of pupae and adults (e.g. Hinton 1981; Rossiter et al. 1988; Hamilton and Zalucki 1993). The reduced weight of last instar larvae of *O. elongata* feeding on *A. alliariae* compared to those on *Cirsium spinosissimum* (devoid of pyrrolizidine alkaloids) might therefore represent a reduction in fecundity and later fitness. We do not want to imply that the relationship between the presence of the alkaloids and reduced larval growth is causal, for other components of plant quality, such as water, nitrogen, sugar or other allelochemicals, might be responsible. Nevertheless, given the present host range, populations living exclusively on either plant are subject to a trade-off between growth and defense.

In other species, estimates of the costs of chemical defense by sequestration have been made by searching for negative correlations between the amount of defensive chemicals in the individuals and either size or growth rate. In both the butterfly *Junonia coenia*, which sequesters iridoid glycosides (Bowers and Collinge 1992), and the sawfly *Neodiprion sertifer*, which sequesters resin acid (Bjorkman and Larsson 1991), there was a suggestion of a cost of sequestration. However, in the butterfly *Euphydryas anicia* which also sequesters iridoid glycosides (Bowers 1988) and the salicylaldehyde-sequestering leaf beetles *Phratora vitellinae* and *Chrysomela vigintipunctata* (Rowell-Rahier and Pasteels 1986) no such costs could be detected. In some cases similar defensive compounds sequestered from the same host plant seem to impose costs on one species but not on another. In the milkweed bug *Oncopeltus fasciatus* sequestration of cardenolides apparently does not involve costs (Isman 1977) and no reduced fitness on milkweeds with higher cardenolide content is evident in the oleander aphid *Aphis nerii* (Groeters 1993). Cohen (1985) found a negative correlation between size and cardenolide content in the monarch butterfly, *Danaus plexippus*, but not in the related queen butterfly *D. gilippus*. The latter sequesters, on average, lower amounts of cardenolides than does *D. plexippus*; however, the difference between the two species persisted when only insects with similar cardenolide contents were taken into account. Cohen argued that *D. gillippus* might be better adapted to the noxious effects of the milkweed hosts.

We believe that *Oreina elongata* provides especially interesting evidence to corroborate such a phenomenon. Within this species two populations show different degrees of adaptation to that host plant which contains allelochemicals appropriate for defense. Larvae of *O. elongata* from the Col du Lautaret population suffered less from feeding on *A. alliariae* than did those from the Mattmark population. The weight just after the third molt was reduced by 24% in the Mattmark population but only by 9% in the Col du Lautaret population, when the larvae were fed on *A. alliariae* throughout development. Thus the Col du Lautaret population, naturally living on *A. alliariae*, is apparently better adapted to this plant than the Mattmark population, which does not encounter this plant in the field. On the other hand larvae from both populations grew equally well on *C. spinosissimum*, and thus adaptation to *A. alliariae* does not influence fitness on the other host.

Adults from the Col du Lautaret population showed no feeding preference for either plant. In contrast, adults from the Mattmark population significantly preferred *A. alliariae*, although they do not encounter the plant naturally. Neither population showed a preference for the locally abundant host, in contrast to findings on host race formation in some other species (e.g. Phillips and Barnes 1975; Fox and Morrow 1981; Wasserman and Futuyma 1981; Scriber et al. 1991). Additionally, in *O. elongata* adult feeding preference and larval performance are not consistent, but seem to be evolving independently. Differences between the behavior (expressed by feeding or oviposition preference) of insect herbivores and their physiology (measured by larval growth rates) have also been described for some butterflies (Chew 1980; Wiklund 1975). Furthermore, positive genetic correlation between behavior and larval performance could not be detected more often than it could be shown to exist (see Fox 1993). In *O. elongata* oviposition preference, as a more reliable trait than feeding preference, could not be established because the females rarely lay their eggs on the leaves, but rather deposit them at the bottom of the vegetation.

As the adults and larvae of both populations are able to sequester pyrrolizidine alkaloids (Dobler and Rowell-Rahier 1994, Pasteels et al. unpubl.) and this is thought to be a derived condition in the genus (Pasteels and Rowell-Rahier 1991), the species presumably fed on *Adenostyles* before a host shift to *Cirsium* occurred. On the other hand, adults of the Col du Lautaret population accepted *C. spinosissimum* in a choice test. With a shift from *Adenostyles* to *Cirsium* the beetles lost the defense by sequestration of pyrrolizidine alkaloids, but this loss might be partially compensated by the mechanical protection against at least vertebrate predators afforded by the very spiny *C. spinosissimum*. Other characteristics of this plant such as its larger distribution range at higher altitudes might provide additional advantages.

The question that remains open is whether the Mattmark population partially lost its tolerance to *A. alliariae*, when this plant ceased to be available, but retained a preference for it, or whether the Col du Lautaret population developed a special tolerance to *A. alliariae*. Gould (1979) showed for herbivorous mites that tolerance to formerly toxic hosts can evolve rapidly. Similarly an increase in expression of detoxification enzyme activity in *Drosophila melanogaster* proved to be inducible within 20 generations (Harshman et al. 1991). Experiments with adults and larvae of *O. elongata* from a habitat with both host plants might provide more insight into the direction in which feeding preference and larval performance are evolving.

We tried to establish whether previous experience with the plant influences larval performance. The comparison of survival and development time between larvae (Mattmark population) raised on *A. alliariae* from hatching on and larvae that were transferred to *A. alliariae* when older, indicates conditioning. If the larvae were fed on *A. alliariae* exclusively, there were no significant differences in survival and instar duration between them and the group on *C. spinosissimum* after 10 days. If they were transferred to *A. alliariae* only after the second molt, the subsequent instar duration was significantly longer and survival worse than in the group that stayed on *C. spinosissimum*. Remarkably, there is no difference in weight on the day of the third molt between the two experiments for the larvae of the Mattmark population on *A. alliariae*, despite the different duration of exposure to this plant. One possible explanation could be that the third instar (not monitored in the constant diet experiment) is the decisively sensitive time during larval development and that the noxious effects of *A. alliariae* express themselves mainly during this time. However, the larvae of the Mattmark population are already 15% lighter after the first 10 days on *A. alliariae*, compared to 24% at the third molt. Our hypothesis is therefore rather that the effect of *A. alliariae* is cumulative over time, and more pronounced for larvae that are not conditioned to it. The similar weights of third-molt larvae from the Mattmark population on *A. alliariae* in the two experiments could also reflect a minimum weight that larvae have to reach prior to the last molt. In both experiments the Mattmark larvae grown on *A. alliariae* molt at this minimum weight. However, the poor development was associated with a shorter exposure to *A. alliariae* in the changeover experiment than in the constant diet experiment (one versus three larval instars). For the Col du Lautaret population no conditioning effect to *C. spinosissimum* is discernible; in both experiments the larvae grew and survived equally well on *C. spinosissimum* and molted with higher weights than on *A. alliariae*.

As both populations perform equally well on *C. spinosissimum*, the data presented here do not support the idea of an ecological trade-off between adaptation to one host and fitness on another. Such an ecological trade-off has often been postulated, but rarely demonstrated (reviewed in Gould 1988; see also Groeters 1993). Instead we suggest that our data provide evidence for a trade-off between growth (on *C. spinosissimum*) and defense (on *A. alliariae*).

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