Geographic variation in oviposition choice of a leaf beetle: the relationship between host plant ranking, specificity, and motivation

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Abstract

The degree of adaptation of herbivorous insects to their local flora is an important component of the evolutionary processes that lead to host plant specialization in insects. In this study we investigated geographic variations in the oviposition preference of the leaf beetle *Oreina elongata* Suffrian (Coleoptera: Chrysomelidae: Chrysolini) in relation to differences in host plant specialization, in the field. We focused on the mechanisms of host choice and asked whether potential differences among populations are due to variations in host plant ranking and/or host plant specificity. We performed a combination of simultaneous choice and sequential no-choice experiments with two of the major host plants of the beetle [*Cirsium spinosissimum* (L.) and *Adenostyles alliariae* (Gouan) (Asteraceae)]. The results suggested that spatial variation in host plant specialization has resulted in differences between populations in some aspects of the oviposition choice of *O. elongata*, while other aspects seem unaffected. We found no variation in host plant ranking among populations, as estimated in simultaneous choice tests. In contrast, the sequential no-choice test indicated that host plant specificity was lower in a population that never encountered the highest ranked plant in the field. This finding agreed with our expectations, and we discuss our results in relation to the commonly used hierarchical threshold model. The results suggested that the mechanism for the differences in specificity is the variation among populations in the general motivation to oviposit, rather than quantitative differences in relative preference for the two hosts. We stress that it is essential to establish which of the two mechanisms is most important, as it will affect the probability of evolutionary change in host plant ranking.

Introduction

The spatial structure of populations and its ecological and evolutionary consequences are central issues in theoretical ecology and evolution (Thompson, 1994; Hanski & Gilpin, 1997; Mopper & Strauss, 1998; Hanski, 1999), and there has been a great interest in the spatial patterns of insect–host plant interactions (Rank, 1992; Thompson, 1994; Mopper, 1998; Mopper et al., 2000; de Jong et al., 2001; de Jong & Nielsen, 2002). This is probably due to long-standing interest in the evolutionary processes that lead to host plant specialization (Futuyma & Moreno, 1988; Jaenike,

1990; Futuyma, 1991; Thompson, 1994; Bernays, 1998), and the realization that the spatial dynamics of insect–plant interactions is often a central component of these processes (Thompson, 1994).

Several lines of evidence have suggested that the oviposition behavior of females may be more important than larval performance in driving the evolution of host specialization, and that selection on the oviposition preferences of herbivorous insects have been studied in some detail (Futuyma, 1983; Thompson, 1988a; Jaenike, 1990; Janz et al., 2001). One important topic in this area has been to describe and understand the decision process that leads an individual female to either accept or reject a given host for oviposition (e.g., Wiklund, 1981; Singer et al., 1992). Experimental results suggest that the oviposition decision

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depends on the hierarchical ranking of the potential hosts according to their general suitability and the instantaneous motivational status of the ovipositing female. This view has been formalized in the hierarchical threshold model of host choice (Courtney et al., 1989), which applies to the typical situation where potential hosts are encountered in sequence. In this model, the ranking of host plants is a consequence of variation in insect preferences for the different plants, which is determined by the stimuli that the insect receives from the plant [we prefer to use the term preference rather than acceptability to describe the insect trait, see Singer (2000)]. The rank hierarchy is thought to be genetically fixed and invariable during the life of an individual female. Whether or not a given female accepts a potential host at encounter will depend on her current motivational status to oviposit, which will typically vary throughout female life (potentially influenced by factors such as egg load, age, or immediate host plant density). The motivational status of a female will constitute the threshold criterion for host acceptance/rejection and it will determine how far down in her host plant hierarchy she will accept hosts at any given time.

The model and its empirical foundations (Wiklund, 1981; Singer, 1983; Thompson, 1988a,b; Courtney et al., 1989) suggest that two insect females could rank two host plants in the same order but still differ in host plant specificity, i.e., the likelihood that the lower ranked plant will be accepted at encounter. Specificity is influenced by two factors in the model: the quantitative difference in preference between the hosts, and rate of change/average level of motivational status (the threshold criterion). The level of preference as well as rate of change in motivational status are likely to lie under genetic control and may respond to natural selection, (e.g., Courtney et al., 1989; Janz, 1998).

We investigated the host plant choices of ovipositing *Oreina elongata* Suffrian (Coleoptera: Chrysomelidae) females from three different populations that vary in host plant specialization in the field. Earlier studies have indicated a strong genetic differentiation among these populations in several developmental traits (age and size at pupation, larval growth rate), but only a relatively limited degree of local adaptation in larval performance on different host plant species (Ballabeni et al., 2003). We expected to find that the differences in host plant availability and utilization among populations would lead to a divergence of oviposition preferences that should be manifested in some of the components of the hierarchical threshold model. These expectations were tested in experiments where two hosts species were presented simultaneously to females, as well as in experiments where these two hosts were presented singly in sequence. We used these two set-ups to estimate the rank order of the two hosts (simultaneous choice trials)

independently of host plant specificity (sequential no-choice trials). Despite the fact that these methods have been used extensively for investigating the oviposition choices of insects, they have only rarely been used together in the same insect species (Funk & Bernays, 2001).

Materials and methods

Study organisms

Oreina elongata is found exclusively in alpine areas at altitudes between 1600 m and 2300 m, and its geographical distribution extends throughout the Alps and further south into the Apennines. Due to its alpine habitat the distribution of *O. elongata* populations is highly heterogeneous, and this is also true within sites, where the occurrence of beetles is patchy. Field observations and mark-recapture studies have strongly indicated that the dispersal rates of *O. elongata* are very low (D. Conconi, unpubl.). The beetles have wings, but despite several years of intense studies, both in the field and in the laboratory, there has been no record of them flying (D. Conconi, unpubl.). Hence, it seems likely that the beetles disperse mainly by walking.

The life cycle of *O. elongata* is adapted to the high alpine environment and includes a 2-year juvenile period as well as the potential for several consecutive reproductive seasons once the adult stage is reached (D. Conconi, unpubl.). The host plant utilization (oviposition, and adult and larval feeding) of *O. elongata* is restricted to three different plant species in the Asteraceae: *Adenostyles alliariae* (Gouan) and *A. glabra* (Miller), as well as the thistle *Cirsium spinosissimum* (L.). Eggs are laid singly on the leaves of host plants continuously from the beginning of July to mid-August (Ballabeni et al., 2001a). Under laboratory conditions a female can lay several hundreds of eggs in a single season (K. Gotthard, unpubl.). Both in terms of morphology and chemistry the *Adenostyles* species are distinctly different from *C. spinosissimum*. Plants in the genus *Adenostyles* produce pyrrolizidine alkaloids (PAs), and both adults and larvae of *O. elongata* (and several other *Oreina* species) sequester PAs and use them as a chemical defense against natural enemies (Rowell-Rahier et al., 1991, 1995; Dobler & Rowell-Rahier, 1994; Pasteels et al., 1995). The third host, *C. spinosissimum*, does not provide the beetles with any sequesterable defensive compounds. In addition to the chemical differences between the host plants, there are substantial morphological differences: the *Adenostyles* species have large, heart-shaped, and relatively smooth leaves while the leaves of *C. spinosissimum* are strongly dentate, hairy, and spiny, which seems to provide protection against predators for the juvenile stages of the beetle (Ballabeni et al., 2001b, K. Gotthard, S. Rasmann, N. Margraf and M. Rahier, unpubl.).

The availability of host plants varies geographically across the Alps, and there are populations of *O. elongata* that only have *Adenostyles* species available in their habitats and others that only have *C. spinosissimum* available, while others again have both an *Adenostyles* species and *C. spinosissimum* present in their habitat. The three populations we used in this study represent these three categories of host plant availability: the population at Col du Lautaret (France, altitude 2058 m) has no *C. spinosissimum* in its habitat, and feeds almost exclusively on *A. glabra*, whereas the population at the Mattmark dam (Switzerland, altitude 2200 m), only has *C. spinosissimum* available and is exclusively found on this plant, finally the population at Col du Petit Saint Bernard (France, altitude 2188 m) has both *A. alliariae* and *C. spinosissimum* in its habitat and all life stages of *O. elongata* can be found on both plants (in the following they will be referred to as the *Adenostyles*, *Cirsium* and two-host populations, respectively). However, females of this two-host population seem to prefer to oviposit on *C. spinosissimum*, which may be due to a higher egg survival on this plant compared to *A. alliariae* (Ballabeni et al., 2001a,b). The shortest distance between any of these populations is at least 200 km, and they are separated by high altitude mountain ranges (3000–4000 m a.s.l.), making dispersal between them very unlikely.

Experimental design – simultaneous choice
During the first week of July 2000 we collected at least 100 adult beetles from each of the three populations, and brought them to a field station close to the two-host population where the host choice experiment was carried out. Prior to the experiments, all populations were given simultaneous access to leaves of *A. alliariae* and *C. spinosissimum* in population cages for at least 1 week to reduce the potential effects of learning in the field sites. The oviposition experiment was performed outdoors in cages made of mesh and plastic (60 × 60 × 60 cm BugDorm-2, MegaView Science Education Services Co., Taiwan) that allowed the weather to affect the ovipositing females. The cages were placed in three rows on flat ground next to the field station, and each row consisted of 10 cages. In every cage a single female was given the choice between *A. alliariae* and *C. spinosissimum*, grown in pots. The plants were placed in the cages so that they had leaf contact, and each female was randomly placed on either of the two plants at the start of the trial. Within each row of cages, the females were randomized with respect to population. We therefore tested 30 females (10 per population) in each 3-day trial, and we performed four such trials. In total we tested 40 individuals per population, and each female was only used once. The potted host plants were reused in the different trials but were randomized over the cages before each trial. At the end of each trial we counted and removed all eggs from the plants.

Experimental design – sequential no-choice
Over a period of less than 1 week at the end of June 2001 (28 June−4 July) we collected at least 150 adults from each of the three populations, and brought them to the field station. Prior to the experiments all populations were given simultaneous access to leaves of *A. alliariae* and *C. spinosissimum* in population boxes over at least 1 week. We used 60 females from each population in the oviposition experiments. These experiments were designed as 'no-choice trials' where each female only had access to one host plant species at a time (*A. alliariae* or *C. spinosissimum*). For logistical reasons, the experiment was performed in the laboratory of the field station where females were placed singly in round plastic cups (10 cm height and 5 cm width) together with one leaf of the host plant. At the beginning of the experiment, females from each population were randomly assigned to one of the two host plant treatments (*A. alliariae* or *C. spinosissimum*), and were left for 48 h. After this first part of the experiment, all females were switched to the alternative host plant and were given the next 48 h to oviposit on this other plant exclusively. At the end of each 48 h trial, we counted the number of eggs that each female had laid on the host plant and elsewhere in the plastic cup. The plastic cups were randomized in a portable shelf system that was placed in one of the windows of the laboratory in order to provide more natural light conditions. The shelves were rotated three times per day to avoid any position effects. The laboratory was left unheated during the experiments, which led to a daily variation in temperature that was similar to the outdoor conditions. During the experiment we measured the temperature in the laboratory three times per day (temperature ranged between 15 °C and 18.5 °C).

Statistical treatment
Throughout the analysis, values for individual females were used as independent observations and we used standard parametric statistical methods. All analyses were performed using StatView 5.0. All proportions were Arcsine-root transformed prior to analysis ($X' = $ Arcsine $(\sqrt{X})$), while egg numbers were Box-Cox transformed when it improved the normality of the data ($X' = ((X + 0.1)^{\lambda} - 1)/\lambda$: to avoid problems with zero-observations when estimating λ, we always performed transformations on X + 0.1, see Sokal & Rohlf, 1995). The values of λ were in each case found by maximum likelihood (Sokal & Rohlf, 1995) and are presented along with the respective analyses.

In the simultaneous choice experiment we first analyzed if the three populations differed in the total numbers of eggs laid and also if there were any effects of trial on oviposition rate. In this ANOVA, we included all females that survived (i.e., also females that did not oviposit during the

trials). In the next step we tested if there was a difference in host plant preference among populations and if it mattered which plant the female was placed on at the start of the trial (start-plant). In this analysis, we used the proportion of eggs that each female laid on *C. spinosissimum* as our measure of host plant preference (i.e., only females that oviposited during the trials were included). We also tested if this measure of host plant preference deviated significantly from 0.5 in any of the populations, which would mean that on average they showed a preference for one of the two hosts presented. Prior to testing, we carefully inspected the forms of the distributions of preference values to check that there were no obvious differences between populations.

In the analysis of the no-choice experiment we used the oviposition on the plants over both time periods to calculate the proportion of eggs that each individual female laid on *C. spinosissimum* during the whole experiment. This data was used to test the effects of population on host plant preference, while controlling for any effects of the sequence in which the plant species were presented to the females. To investigate mechanisms of potential differences in host specificity we also analyzed the two time periods separately (before and after the switch). Throughout the experiment an unexpectedly large proportion of the eggs was deposited on the plastic boxes where they were kept during the experiment. Because of this we calculated the proportion of the total amount of eggs that each female deposited on the plant it had available, and performed the analysis on that measure. To correct for multiple testing we performed sequential Bonferroni-adjustments to keep the table-wide level of α at 0.05 (Rice, 1989).

Results

Host plant ranking in the simultaneous choice experiment

Ten of the 120 females used in the experiment died during the trials (one, three, and six from the three populations) and of the surviving females, between 24 and 27 females per population laid eggs. Some of the individuals that did not oviposit may have been mis-sexed males. Including all surviving adults, there was a significant effect of trial starting date on the number of eggs laid but there was no significant difference between populations (ANOVA on Box-Cox transformed total egg number ($\lambda = 0.132$): start date: $F_{3,98} = 6.88$, P<0.001; population $F_{2,98} = 2.22$, P = 0.11; interaction $F_{6,98} = 1.05$, P = 0.40). In all populations there was a similar decrease in oviposition with the progression of season that was consistent with the pattern found in the field (Ballabeni et al., 2001a).

In the analysis of host plant ranking we only included females that oviposited during the trials, and neither population nor start-plant had significant effects on host plant
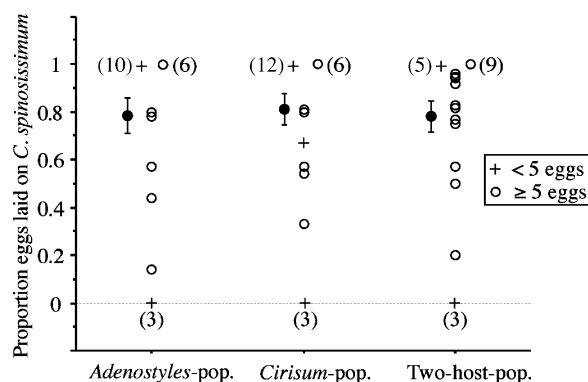

Figure 1 Results from the simultaneous choice experiment showing the proportion of eggs that each female laid on *C. spinosissimum*. Circles denote females that laid five or more eggs while plus signs denote females that did oviposit but laid fewer than five eggs. The numbers of females that had identical values are given in brackets next to the symbol. Filled circles denote population means ± SE.

preference (Figure 1; ANOVA on arcsine-root transformed values: population, $F_{2,71} = 0.14$, P = 0.87; start plant, $F_{1,71} = 1.13$, P = 0.29; interaction, $F_{2,71} = 0.77$, P = 0.47). However, all three populations significantly preferred *C. spinosissimum* to *A. alliariae* (t-test for difference from the arcsine-root transformed value of 0.5; *Adenostyles* population: t = 3.72, d.f. = 23, P = 0.0011; *Cirsium* population: t = 4.52, d.f. = 26, P = 0.0001; two-host population: t = 3.83, d.f. = 25, P = 0.0008). There were no apparent differences between populations in the form of the preference distributions. Arguably, the measure of host plant preference used here (proportion of eggs laid on a certain plant species) is better estimated in females that lay many eggs. We therefore performed a new set of identical analyses where we only included females that laid more than five eggs during their trials. However, in these analyses the effects of population and start plant were also non-significant, while all populations significantly preferred *C. spinosissimum* to *A. alliariae*. Since the reanalysis did not change any of the conclusions from the analysis of the whole data set it is not presented in detail.

Host plant specificity in the no-choice experiment

A total of 17 of the 180 adults used in this experiment did not oviposit during any of the time periods, and they were excluded from the data. Most of these individuals were probably males that were included in the experiment because of mistakes in the sexing procedure. Excluding these individuals, the total number of eggs laid per female during both experimental periods ranged from 11 to 59 (mean ± SE: 37.9 ± 0.7)
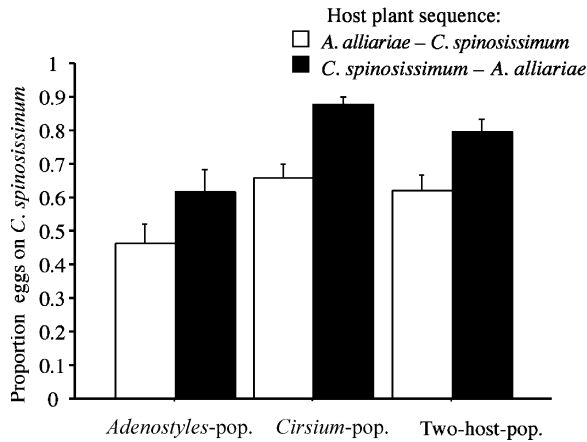
Figure 2 Results from the sequential choice experiment showing the mean proportion of eggs (+ SE) that each population laid on *C. spinosissimum* during both time periods of the experiment. The result for each host plant sequence is shown separately.

As a composite measure of relative preference, we calculated the proportion of eggs that each female laid on *C. spinosissimum* across both hosts during the whole experiment. This proportion was strongly affected by both population and the sequence in which the plants were presented to the beetles (Figure 2; ANOVA on arcsine-root transformed proportions: population, $F_{2,156} = 11.10$, $P<0.0001$; start plant, $F_{1,156} = 22.79$, $P<0.0001$; interaction $F_{2,156} = 0.20$, $P = 0.82$). The post-hoc test revealed that there were no significant differences between the *Cirsium* and two-host populations, while both these populations showed a significantly higher preference for *C. spinosissimum* than did the *Adenostyles*-population (Scheffe's test for C-TH: $P = 0.42$, *Adenostyles*-*Circium*: $P<0.0001$, *Adenostyles*-two-host: $P = 0.0043$). The effect of plant sequence was due to a stronger preference for *C. spinosissimum* in all populations when this plant was presented first (Figure 2).

To perform a more detailed analysis of the components of specificity, we calculated the proportion of eggs that each female laid on the available plant (as opposed to eggs laid on the box) during each time period of the experiment (before and after the plant switch). The analysis of this measure showed significant effects of population and plant as well as of the interaction between these factors on the proportion of eggs laid on the plants (Figure 3; ANOVA on arcsine-root transformed values for the first period: population, $F_{2,157} = 18.69$, $P<0.0001$; plant, $F_{1,157} = 33.47$, $P<0.0001$; interaction $F_{2,157} = 12.19$, $P<0.0001$; for the second period: population, $F_{2,157} = 10.64$, $P<0.0001$; plant, $F_{1,157} = 67.13$, $P<0.0001$; interaction $F_{2,157} = 10.04$, $P<0.0001$). Identical analyses on the number of eggs laid on the plants gave qualitatively the same result and are not therefore shown. The consistent significance for the inter-action term indicates that the *Adenostyles* population behaves differently compared with the other populations. In both time periods, females from the *Cirsium* and two-host populations laid more eggs on *C. spinosissimum* than on *A. alliariae*, while for the *Adenostyles* population there was no such difference between host plant treatments.

All populations laid significant numbers of eggs on the plastic box (Figure 3), but during both time periods the pattern of oviposition on the box was largely a mirror image of the oviposition on plants. When *C. spinosissimum* was available in the box, the females from the *Cirsium* and two-host populations laid a significantly lower proportion of their eggs on the plastic compared to the situation when they only had *A. alliariae* available, whereas females from the *Adenostyles* population deposited a majority of their eggs on the plastic, independent of host plant treatment (Figure 3).

Discussion

The results suggest that some aspects of the oviposition preference of *O. elongata* varies amongst these populations, while other aspects seems to be unaffected by the differences in natural host plant use. We found no difference in host plant ranking among populations when it was estimated in simultaneous choice tests. All populations significantly preferred *C. spinosissimum* to *A. alliariae* (Figure 1), which
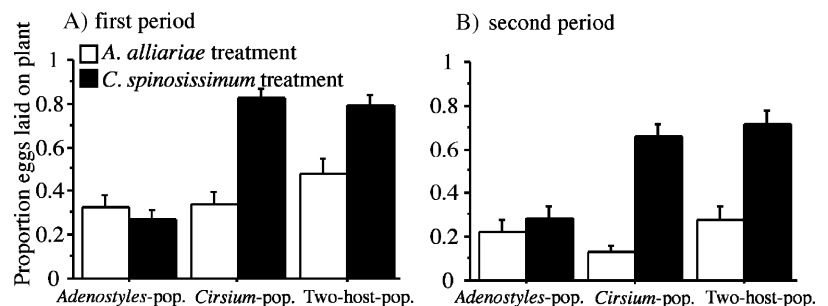
Figure 3 Results from the sequential choice experiment showing the mean proportion of eggs (+ SE) laid on the plants separated by populations and host plant treatment during (A) the first period, and (B) the second period after the host switch.

raises questions concerning *Adenostyles* populations that never encounter *C. spinosissimum* in its habitat. The pattern of oviposition in the no-choice experiment confirmed the preference for *C. spinosissimum* over *A. alliariae* in the *Cirsium* and the two-host populations, while the oviposition of the *Adenostyles* population was unaffected by host plant treatment when the two hosts were presented in sequence (Figures 2 and 3). This result suggests that the *Adenostyles* population is less specific in its choice between these two hosts compared to the other populations.

In the no-choice experiment, females from all three populations deposited unexpectedly large numbers of eggs on the plastic boxes rather than on the plants (Figure 2). To what extent females oviposit on other objects than the host plants in the field has not been studied in detail, and at present we cannot exclude that is does happen. However, it seems likely that the oviposition off the plants here was a consequence of the limited space of the containers in combination with high oviposition rates. Nevertheless, the consistently significant difference between the *Adenostyles* population and the other two in the no-choice experiment indicates that the absence of the highest ranked host in the natural habitat has affected oviposition decisions.

The lower host plant specificity of the *Adenostyles* population (Figure 2) agreed with our expectations, since these females will never encounter the higher ranked *C. spinosissimum* in the field and selection should work against

individuals that continuously reject suitable *Adenostyles* plants. However, we expected that the mechanism for this low specificity would be an increased acceptance rate of *Adenostyles* plants in the *Adenostyles* population, simply because the acceptance/rejection of *Adenostyles* plants is the only trait that is expressed in this population. The result of the no-choice experiment does not support this expectation, since the population difference is not due to variation in the *A. alliariae*-treatment and there is no indication that the preference for *A. alliariae* is higher in the *Adenostyles* population than the other two populations (Figure 3). The main difference between the *Adenostyles* population and the other two was instead that it was less likely to oviposit on *C. spinosissimum* when this was the only plant available (Figure 3).

Hence, the *Adenostyles* population combines a high preference for *C. spinosissimum* (Figure 1) with a low specificity for the choice between this plant species and the *Adenostyles* plants (Figure 2), and the difference is not due to quantitative variations in the preference for *A. alliariae* (Figure 3). An interpretation of these results which complies with the hierarchical threshold model suggests that a potential mechanism for the difference in specificity is that females of the *Adenostyles* population have a generally higher motivation to oviposit than females from the other two populations (see Figure 4 for a graphical representation). It implies that in the no-choice experiment, the motivational threshold of the *Adenostyles* population females constantly moved in a range of very low acceptance values,
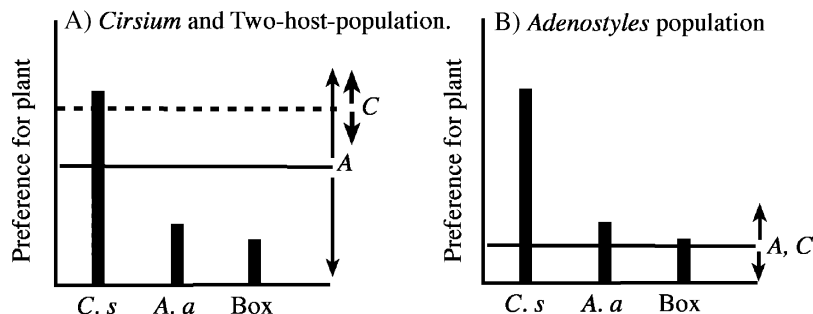

Figure 4 Interpretation of the results in relation to the hierarchy threshold model when the difference between populations was due to variation in motivation to oviposit, for (A) the *Cirsium* and two-host populations and (B) the *Adenostyles* population. Plant species are abbreviated on the *x*-axis (*C. s*: *C. spinosissmum*, *A. a*: *A. alliariae*). The horizontal lines in each graph represent examples of acceptance thresholds, and the thresholds are separated by host plant treatment in (A) (*C. spinosissimum* = *C*, dashed; *A. alliariae* = *A*, full). Note that the thresholds represent the motivation of a female at a given instance, and they may move both down (when searching for a host) or up (after oviposition) during the experiment. The arrows to the right of each graph show, for each host plant treatment, the region within which the motivational threshold typically moved during the experiments. The upper limit of the range within which each threshold-line moved is determined by the general motivational level/speed of increase in motivation during the search for oviposition sites, whereas the lower limit is determined by host plant treatment. For example, a female with any of the motivational thresholds depicted in (A) would only accept *C. spinosissimum* for oviposition, but if this plant was not available, the threshold will descend in the graph until she starts accepting other oviposition sites at encounter. When she eventually oviposits, the threshold may move up again and she will perhaps again reject the lower ranked plants for some time. In contrast, the female in (B) would at this point accept all the oviposition sites depicted and due to her genetically high level of motivation her threshold would only rise very little after oviposition, and then start to descend again.

leading to equal acceptance rates for both plants and a frequent acceptance of the plastic box (Figure 4b).

Since the experimental females were field collected, we cannot rule out the possibility that the variation in host specificity was due to environmentally induced differences rather than a genetic variation among populations. In any case, it is possible that the total absence of the highest ranked host in the *Adenostyles* population led to a reduced 'choosiness' by an increase in the general level of motivation to oviposit. In the natural situation, beetles in the *Adenostyles* population spend practically all their time on, or very close to *A. glabra*, and even with a very high motivational level, eggs will practically always end up on or very near this plant. In relation to this it is interesting to note that in a study of the butterfly *Euphydryas editha*, Singer et al. (1992) found that the motivation to oviposit was higher in a population where the highest ranked host plant was naturally absent than in a population where it was naturally available. Indeed, Courtney et al. (1989) proposed that differences in host specificity should typically evolve by genetic modifications of the motivational level rather than by changes in preferences for different host plants. However, there is no a priori reason to believe that these two evolutionary mechanisms are mutually exclusive, and oviposition choices may evolve by a combination of changes in relative preferences and changes in motivational level (Singer et al., 1992).

Studies of the spatial variation in oviposition preferences of phytophagous insects in relation to variations in host plant availability have produced results ranging from essentially no genetic differentiation among populations at a wide spatial scale to a high degree of local specialization on a small spatial scale (Thompson, 1988b, 1994; Singer et al., 1993, 1994; Wehling & Thompson, 1997; Peterson & Denno, 1998; Thomas & Singer, 1998; Pappers et al., 2002). As it appears that *O. elongata* never flies, it is highly improbable that there is gene flow among the populations investigated here, and there are genetic differences among these populations in neutral genetic markers (N. Magraf and M. Rahier, unpubl.), as well as several developmental traits such as larval growth rate and body size (Ballabeni et al., 2003). Although we cannot conclude that the difference found here has a genetic basis, the results still indicate that there is a variation among populations in host specificity and that this may be due to a difference in the general motivation to oviposit rather than to quantitative differences in relative preference for the two hosts. For the evolution of insect host utilization it may be essential to determine which of these mechanisms are most important, because changes in relative preference may ultimately lead to evolutionary changes in host plant ranking, while changes in motivational level will not necessarily affect ranking at all.

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