

Evolution of host-selection behaviour in insect herbivores: genetic variation and covariation in host acceptance within and between populations of *Choristoneura rosaceana* (Family: Tortricidae), the obliquebanded leafroller

Y. CARRIÈRE* & B. D. ROITBERG

Center for Pest Management and Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, BC, Canada V5A 1S6

Populations of insect herbivores exploiting habitats that differ in host species composition may experience selection for divergent host-selection behaviour. To assess potential genetic constraints on the evolution of host-selection behaviour in such populations, we estimated genetic variation and covariation in larval acceptance of different host species within and between populations of the obliquebanded leafroller, *Choristoneura rosaceana*. Host-acceptance behaviour was analysed using the threshold model of quantitative genetics. According to this model, there is a continuously distributed variable describing the motivational/physiological state of individuals in the population, and a threshold of acceptance representing the acceptability of a host species. Individuals in which this variable exceeds the threshold accept the host while individuals below the threshold reject it. Parent–offspring regressions, a selection experiment, and comparisons of full-sibs in three pairs of populations revealed significant additive genetic variation in host acceptance. Genetic correlations between the responses to different hosts were either positive or not significantly different from zero, suggesting that local change in host acceptance will not favour behavioural specialization in populations of *C. rosaceana*. The pattern of the reaction norms for host response in the pairs of populations confirmed that divergence in host-selection behaviour does not involve behavioural specialization in the obliquebanded leafroller.

Keywords: *Choristoneura rosaceana*, genetic correlation, heritability, host-selection behaviour, quantitative genetics, threshold trait.

Introduction

The frequency and suitability of host plant species encountered by insect herbivores can vary in space and time because of heterogeneity in the environment, disturbance, colonization and intra- or interspecific interactions (Thompson, 1985; Singer, 1986). Such variability could favour change in host-selection behaviour, and result in genetically-based divergence in diet among populations of plant-feeding insects (Otte & Joern, 1977; Jaenike, 1978; Courtney, 1982; Futuyma, 1983; Rausher, 1984; Ward, 1987; Jaenike

& Holt, 1991). Indeed, many studies have reported evidence of such divergence among populations of insects in response to host plants (Table 1).

The potential of a population to undergo selective change in host-selection behaviour is determined by four factors: (i) the amount of phenotypic variation in host-selection behaviour, (ii) the genetic basis of such variation, (iii) the relationship between host-selection behaviour and fitness (Singer *et al.*, 1989; Jaenike, 1990; Carrière & Roitberg, unpublished observations), and (iv) migration that must be low enough to allow genetic divergence of the norm of reaction for host response (Futuyma & Peterson, 1985; Bossart & Scriber, 1995; Carrière & Roitberg, unpublished observations). Genetic correlations between responses

*Correspondence: Department of Biology, McGill University, 1205 Dr Penfield Avenue, Montreal, Quebec, Canada H3A 1B1.

Table 1 Among-population comparisons suggesting genetically based variation in host-selection behaviour in plant-feeding insects

Order	Character	Reference
Coleoptera	Feeding preference	Harrison (1987); Rowell-Rahier (1984)
	Oviposition preference	Wasserman (1986)
Diptera	Oviposition preference	Jaenike & Grimaldi (1983); Prokopy <i>et al.</i> (1988); Tavormina (1982)
Lepidoptera	Larval host-selection	Futuyma <i>et al.</i> (1984); this study
	Oviposition preference	Bossart & Scriber (1995); Phillips & Barnes (1975) Schneider & Roush (1986); Thomas <i>et al.</i> (1987); Thompson (1993); Singer <i>et al.</i> (1992); Singer & Parmesan (1993)

to different hosts could influence the evolution of diet (Arnold, 1981; Singer *et al.*, 1992). For example, a positive genetic correlation between acceptance of a highly suitable host and of a toxic host could contribute to maintaining both hosts in the insect diet for an extended period if the toxic host is rare, or could lead to rapid avoidance of both hosts if the unsuitable host is abundant (Levins & MacArthur, 1969; Futuyma, 1983; Fox & Lalonde, 1993). Since genetic correlations between the responses to different hosts have rarely been estimated (Wasserman, 1986; Courtney & Hard, 1990; Thompson, 1993), it is difficult to assess their importance in constraining diet breadth. The goal of this study was to estimate the heritabilities and genetic correlations of responses to different hosts in a species of plant-feeding insect, and to see whether these genetic parameters could be used to understand evolutionary change in its host-selection behaviour.

Local abundance of a single host species may result in diet specialization (Tavormina, 1982; Futuyma, 1983; Ward, 1987). Insect populations exploiting agricultural crops are subdivided among large patches of single hosts. When gene flow is low among patches, evolution of host-selection behaviour may occur independently in the populations exploiting different patches (Via, 1990). In this context, genetic correlations between acceptance of a host grown in a monoculture and acceptance of hosts that are absent in the monoculture may favour evolutionary change in diet breadth. Negative correlation between acceptance of hosts may result in behavioural specialization following the evolution of increased host acceptance in a monoculture, since migrants from the monoculture would then have reduced acceptance of other hosts. Positive or null correlations, however, could favour polyphagy, since increased acceptance of the host grown in the monoculture would result in increased acceptance of other hosts, or leave the response to these hosts unchanged.

In British Columbia, Canada, the obliquebanded leafroller, *Choristoneura rosaceana* (Harris), is a generalist herbivore that can exploit diverse agricultural crops and forests (Carrière, 1992a,b; Carrière & Roitberg, 1994). Host selection is conducted by females that can fly and lay egg batches on the surface of host leaves, or by newly hatched larvae that can disperse on silk threads and sample many host species before settling. In Lepidoptera, larval dispersal results mainly in intrahabitat movements (Roff, 1990a; Thompson & Pellmyr, 1991), and the same appears to be true for the obliquebanded leafroller (Gillespie, 1982; Carrière, 1992c). Therefore, even if *C. rosaceana* females determine to some extent the environment of their offspring, the behaviours of the larvae are likely to play an important role in host selection.

A previous study of the obliquebanded leafroller demonstrated that newly hatched larvae strongly discriminate among different host species, and suggested significant variation among larval genotypes in host-selection behaviour (Carrière, 1992c). The present study addresses the following three specific questions. (i) Is variation in larval host-acceptance genetically based in *C. rosaceana*? (ii) What is the pattern of the genetic correlations between responses to different hosts? (iii) Is local evolutionary change in host-selection behaviour favouring diet specialization or generalization in this species?

Materials and methods

Bioassay to measure larval host-acceptance

Host acceptance (*sensu* Singer, 1986) is measured by monitoring the response of an insect encountering a single host. Since acceptance estimates the response of an insect to a specific host (= environment), and *C. rosaceana* larvae contact plants sequentially in their natural host-search behaviour, host acceptance data

are perfectly suited to calculating heritability of, and genetic correlations between, responses to different host species.

The following sequential protocol was employed to measure host acceptance (Carrière, 1992c): (i) 10 larvae were transferred to the leaf surface of each branch of the host(s); (ii) the branches were placed under perforated plastic containers (diam. 27.5 cm, height 30.5 cm) lined up in front of fans; (iii) the larvae were allowed to settle for 2 min; (iv) the fans were started; and finally (v) the numbers of larvae remaining on the branches were counted after 60 min. Care was taken such that the plants did not contact the containers and that no larvae fell off the plants before the fans were started. Insects were defined as having 'accepted' or 'rejected' a host if they were respectively on or off that host after 60 min.

This bioassay had already been used to conduct two experiments (Carrière, 1992c). First, full-sib families were each divided into five groups that were simultaneously placed on four host species and on a control (a plastic 'plant'). This showed that variation in host acceptance was the result of host-selection behaviour and not of a host-independent propensity to move, because the larvae preferred three of the four plant species over the control. Secondly, full-sib groups were each divided in two and acceptance of apple branches was measured simultaneously in the laboratory or in the field (field larvae were counted 8 h after being placed on a tree). Apple acceptance measured in the two environments was found to be significantly and positively correlated, demonstrating the relevance of our laboratory bioassay.

This bioassay was used to estimate the heritability of apple (*Malus domestica*) acceptance, and to compare host-selection behaviour between pairs of populations of *C. rosaceana*, or between lines that had been selected for increased or decreased acceptance of broad bean plants (*Vicia faba*). The bioassay was modified slightly (see below) to conduct the selection experiment. The larvae used in the bioassays (conducted at $24 \pm 1^\circ\text{C}$) were less than 2 h old, naive (i.e. they had not encountered any host), and starved. The first egg mass of females was placed, prior to hatching, at a temperature of $7.5 \pm 1^\circ\text{C}$, a relative humidity near 100 per cent, and under a 16 L:8 D photoperiod. This procedure (not used in the parent-offspring experiment below) synchronized hatching with light onset and facilitated control of larval age in the bioassays. All insects were raised on an artificial pinto bean diet (modified from Shorey & Hale, 1965), and unless otherwise stated, at a temperature of $25 \pm 1^\circ\text{C}$ under a 16 L:8 D photoperiod.

Heritability of apple acceptance

The proportion of larvae accepting a host within a family is approximately normally distributed within *C. rosaceana* populations (Carrière, unpublished data), and therefore host acceptance was assumed to be a threshold character (Mackay & Doyle, 1978; Falconer, 1981). In this model, acceptance (or rejection) of a plant species is assumed to be determined by the interaction of a normally distributed underlying variable and a threshold. The distribution of the underlying variable represents the variation among individuals in their motivational/physiological state. The position of the threshold represents the level of the motivational/physiological state above which a specific host is accepted. In this study, the threshold is assumed to be identical for all plants of a given species, but to vary among host species of different acceptability (*sensu* Singer, 1986). The underlying trait is assumed to be inherited in a typical polygenic manner (Falconer, 1981).

A parent-offspring regression technique (Roff, 1986) was used to estimate the heritability of apple acceptance (Introduction; objective i). Moths from the fifth generation of a colony (~300 individuals collected from an apple orchard initiated a colony subsequently maintained at ~200 breeding individuals) were arbitrarily paired to provide parental families (the F_1). Apple acceptance was estimated in each F_1 family, and 30 larvae from each family were raised to adulthood. The F_1 moths were mated assortatively with respect to host response and apple acceptance was then measured in the F_2 . Ten replicates (i.e. 100 larvae) were used to estimate apple acceptance in a given family.

The calculations of heritability were based on the pooled results of the 10 replicates conducted for each F_1 or F_2 family. Heritability estimates derived using single parental values were corrected for assortative mating using the formula given by Falconer (1981, p. 164), where family values of the F_1 generation were used to estimate the correlation between parents (Roff, 1990b).

Selection for increased or decreased acceptance of broad bean

This experiment was undertaken to confirm whether host acceptance is heritable (Introduction; objective i), and to determine whether direct selection on acceptance of one host may result in correlated responses in acceptance of other hosts (Introduction; objective ii).

Bean-acceptance behaviour was estimated in the same manner as apple acceptance, except that (i)

smaller containers (diam. 21.5 cm, height 13.5 cm) were used to facilitate recovery of larvae that had left the plant, and (ii) larvae remaining on the plants were counted after 30 min to increase the number of families that could be measured. Bean plants (between 20 and 30 cm) were cut and trimmed to bare their third and fourth pairs of unfolded leaves, and inserted in florist vials before receiving the larvae. Sixty larvae per family (six replicates) were measured. Larvae found on the plant or crawling in the containers at the end of a bio-assay were respectively designated as 'stayers' or 'leavers'. For each of the 16 families selected to provide parents in a given generation (see below), 20 'stayers' (for families with the highest bean acceptance) or 'leavers' (for families with the lowest bean acceptance) were raised.

Bean acceptance was initially estimated in 24 families of the fifth generation of a colony (sampling and rearing procedures as above). The 'stayers' from the eight families with the highest bean acceptance were crossed to produce a line with increased bean acceptance, and 'leavers' from the eight families with the lowest bean acceptance were crossed to produce a line with decreased bean acceptance. In two subsequent generations of selection, bean acceptance was initially measured in 13–24 families within each line. Individuals from the eight extreme families in each line were then retained for the crosses.

To investigate whether selection on bean acceptance resulted in correlated responses to other hosts, individuals from lines selected for three generations were simultaneously tested on bean plants, and on apple and wild rose branches (*Rosa* sp.). Three replicates (i.e. 30 larvae) were used to measure simultaneously acceptance of each host in a family. Potted bean plants bearing second to fourth unfolded leaf pairs were utilized in these tests.

Variation in host acceptance (arcsine square-root transformed) in the first two generations of selection was analysed using one-way ANOVAs with Family nested within Line and considered as a random effect. Line was considered a fixed effect. Host acceptance (arcsine square-root transformed) in the third generation of selection was analysed using a two-way ANOVA where Host and Line were considered fixed effects and Family nested within Line a random effect. Family-mean correlations were computed to estimate within-line genetic correlations in acceptance of host pairs (Via, 1991).

Comparison between pairs of populations

These experiments were conducted to estimate genetic correlations between responses to different hosts (see Introduction; objective ii), and to assess whether

populations exploiting different habitats diverged in their host-selection behaviour (see Introduction; objective iii). For each pair of populations larval responses were estimated on two hosts, each host being locally abundant and/or uniquely present in the habitat exploited by one of the populations.

In the first comparison, larval responses to apple and cherry branches (*Prunus* sp.) were compared between two populations collected in an apple and a cherry orchard at Winfield, BC (hereafter, Apple and Cherry populations). The populations were separated by less than 1 km, which is within the flight range of moths. No apple trees were grown in the cherry orchard but some were found in its proximity (within 400 m). Similarly, few cherry trees were found around the apple orchard. Leafrollers had been present in the apple and cherry orchards for at least 10 and six generations, respectively.

In the second comparison, larval responses to apple and blueberry branches (*Vaccinium corymbosum*) were compared between a population collected from a blueberry field at Pitt Meadows, BC ('site 2' studied by Gillespie (1982)), and insects originating from an apple orchard at Oliver, BC (hereafter, Blueberry and Apple populations). Assuming that no population extinction had occurred since Gillespie's study, the Blueberry population had been present for at least 20 generations. The history of the Oliver population is unknown. The populations were separated by 400 km and the Cascades mountain range. No apple orchards were seen in the vicinity of the blueberry field (over at least 10 km), nor was blueberry grown in the valley in which the apple orchard was located (over at least 100 km).

The last comparison was between larvae from an apple orchard at Winfield, BC, and a population collected in a mixed forest near Apex Mountain, BC, about 250 km away (hereafter, Apple and Mixed forest populations). Leafrollers had been present in the mixed forest and the apple orchard for at least four and 10 generations, respectively. Many hosts palatable to *C. rosaceana* were abundant in the forest, but larvae were only found on mockorange (*Philadelphus lewisii*) and red-osier dogwood (*Cornus stolonifera*). Apple and mockorange were chosen to compare larval responses between the populations. No apple trees were grown in the area surrounding the mixed forest (over at least 14 km) and mockorange was not seen in the vicinity of the apple orchard in Winfield (that orchard was surrounded by other apple orchards).

To avoid possible non-Mendelian parental effects, host-selection behaviour was measured in the F_2 from field-collected insects. The F_1 of the Blueberry population was reared at 19°C for approximately 2 weeks to synchronize insect phenology in the Blueberry and

Apple populations. Nine and seven mating pairs, respectively, provided eggs to establish the Blueberry and Mixed forest colonies, whereas over 95 mating pairs started the colonies from the orchards. Such a difference results from the low population densities in the blueberry field and mixed forest.

Host acceptance in a family was simultaneously measured on two hosts, using at least four replicates (40 larvae) per host. Plant material used in the bioassays was collected either at the sites where the populations had been sampled (Mockorange and Blueberry populations), or at the Agriculture Canada Summerland Research Station. McIntosh (apple) and Lambert (cherry) cultivars were used in the tests because they were dominant in the orchards where the populations had been collected. The branches of each host species were arbitrarily sampled from at least 20 plants, and were used only once in the bioassays. Freshly cut branches were employed, except for mockorange and blueberry branches that were kept in water (at 7.5°C, 16 L:8 D) for a maximum of three and nine days, respectively, before being used.

The variation in host acceptance (arcsine square-root transformed) in each pair of populations was analysed using two-way ANOVAs with Population and Host treated as random and fixed effects, respectively, and Family nested within Population as a random effect.

Family-mean correlations were computed to estimate within-population genetic correlations in acceptance of host pairs. These correlations reveal potential genetic constraints on the evolution of norms of reaction in host-selection behaviour (Via, 1991). To increase statistical power, a single correlation was calculated for the apple-cherry population-pair. Pooling was done on the assumption that the populations were sympatric, and because they did not differ statistically in their genetic correlations between the responses to the hosts (Sokal & Rohlf, 1981, p. 589). The genetic correlations were estimated separately within the other populations.

Results

Heritability of apple acceptance

Apple-acceptance behaviour had a high heritability (Table 2). The estimates calculated using male or female parental values were similar to the estimate obtained using mid-parent values. This suggests that non-Mendelian parental effects did not influence larval acceptance in this experiment (Falconer, 1981; Carrière, 1994).

Table 2 Heritability of apple-acceptance behaviour in *Choristoneura rosaceana*

Regression	h^2 (SE)
On male parent	0.76 (0.31)*
On female parent	0.82 (0.26)**
On mid-parent	0.73 (0.17)**

* $P = 0.0047$, ** $P < 0.0003$, d.f. = 1,27.

Direct and correlated responses to selection

Bean-acceptance behaviour differed significantly between the lines after just one generation of selection, and significant variation among the families in host-selection behaviour was detected in the first two generations of selection (Fig. 1, Table 3). This indicates significant additive genetic variance for bean-acceptance behaviour within the selected population.

After three generations of selection, the lines still had significantly different bean-acceptance behaviour, and significant among-family variation in host-selection behaviour was detected (Tables 4, 5). The host species were not equally preferred by the larvae, but the difference in host acceptance between the lines was apparently maintained across the three host species (Table 5; Host \times Line effect). This suggests that direct selection on broad bean acceptance had indirect effects on the response to the apple or rose hosts, and therefore that positive genetic correlations in response to the bean-apple and bean-rose host pairs were present within the selected lines. Five of the six genetic correlations estimated within the selected lines were positive (mean = 0.19, SE = 0.07), but none was significantly different from zero (at $P < 0.05$).

Comparison of pairs of populations and estimates of genetic correlations in acceptance of host pairs

Each host was on average equally acceptable to larvae in each pair of populations (Table 6). The Family effect was the only significant source of variation in the comparison of the Apple and Cherry populations (Table 6; Fig. 2a), suggesting significant genetic differences among families in their average host acceptance. The genetic correlation between acceptance of the apple and cherry hosts was positive but not significantly different from 0 ($r = 0.38$, $P = 0.07$, $n = 23$). Separate analysis on the Apple and Cherry populations yielded qualitatively similar results; both genetic correlations between acceptance of the apple and cherry host were

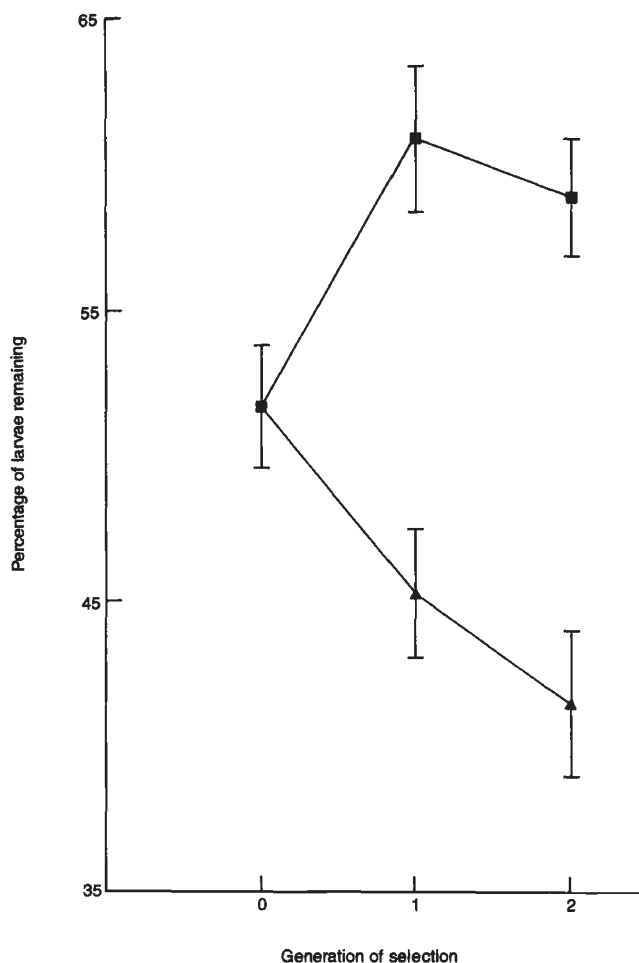


Fig. 1 Broad bean acceptance (% ± SE) in the base population of *Choristoneura rosaceana* and in the first two generations of selection. Triangles, selection for lower acceptance. Squares, selection for higher acceptance. Different bioassays were used to estimate host responses in the first two and in the third generations of selection. Therefore, host responses measured after three generations of selection are presented in Table 4.

Table 3 ANOVAS to compare variation in *Choristoneura rosaceana* larval acceptance of broad bean in the first two generations of selection

Source	d.f.	SS	MS	F	P
First generation of selection					
Line	1	1.52	1.52	54.73	<0.0001
Family (Line)	33	2.11	0.0639	1.92	0.0037
r^2	0.37				
Second generation of selection					
Line	1	2.34	2.34	68.61	<0.0001
Family (Line)	40	3.90	0.097	2.86	<0.0001
r^2	0.47				

r^2 measures how much variation in the dependent variable is accounted for by the model.

positive, but not significantly different from zero ($P < 0.05$).

Comparison of the Apple and Blueberry populations revealed a significant Population effect (Table 6), indicating that individuals from the blueberry field had a higher tendency to accept the hosts than larvae from the apple orchard (Fig. 2b). The nonsignificant Population × Host effect indicates that the norms of reaction were parallel. The genetic correlations between the responses to the apple and blueberry hosts were positive but not significant in the two populations (Apple population: $r = 0.30$, $P = 0.39$, $n = 10$; Blueberry population: $r = 0.36$, $P = 0.31$, $n = 10$).

In the third comparison, the norms of reaction of the Apple and Mixed forest populations were not parallel (Table 6: Pop × Host effect; Fig. 2c). The members of each population showed a similar acceptance of mockorange ($t = -0.76$, d.f. = 16, $P = 0.46$), but insects

Table 4 Host-acceptance behaviours of *Choristoneura rosaceana* after three generations of selection on broad bean acceptance

Host	Line	X	SE
A	L	46.5	2.7
	S	54.4	4.5
B	L	59.2	2.6
	S	74.9	2.2
R	L	41.9	2.9
	S	49.7	2.9

The average ($X \pm SE$) of the percentage of larvae that accepted a host within the families of each line is presented. Fourteen and 13 families were respectively measured in the line selected for increased (S) or decreased (L) acceptance of bean. The host species were apple (A), broad bean (B), and rose (R).

from the apple orchard had much higher acceptance of apple than insects from the mixed forest ($t=3.47$, $d.f. = 16$, $P=0.003$). The genetic correlations between acceptance of the pair of hosts were positive but only significantly different from 0 in the population from the mixed forest (Apple orchard: $r=0.33$, $P=0.38$, $n=9$; Mixed forest: $r=0.68$, $P=0.04$, $n=9$).

Discussion

The existence of genetic constraints on growth, survival, and reproduction (hereafter, performance) across phytochemically different hosts is central to many models of the evolution of diet breadth, sympatric speciation and the maintenance of genetic variation in insect herbivores (Jaenike, 1981; Diehl & Bush, 1984; Rausher, 1984; Futuyma & Peterson, 1985; Jaenike & Holt, 1991; Fox, 1993; Carrière & Roitberg, 1994; Bossart & Scriber, 1995). In such

models, genetically based trade-offs in performance on different hosts are assumed to slow the joint evolution of high performance across the potential hosts of a population (Via, 1987). Therefore, in the presence of genetic variation in host-selection behaviours, (i) preference or avoidance of some hosts may evolve at a faster rate than performance on these same hosts, thereby favouring specialization in diet, or (ii) selection may produce genetic correlations between preference and performance, thereby favouring sympatric speciation. In the present paper, we consider genetic constraints that may directly affect host-selection behaviours. Negative genetic correlations between the responses to different host species would be expected to result in trade-offs in discrimination within these host species (Singer *et al.*, 1992; Fox & Lalonde, 1993). If abundant, such correlations could partly explain why the majority of insect herbivores have a specialized diet (Jaenike, 1990).

Table 5 ANOVA to compare variation in host-acceptance behaviour between the selected lines of *Choristoneura rosaceana* after three generations of selection

Source	$N_{d.f.}$	$D_{d.f.}$	F	P
Host	2	159	37.33	0.0001
Family (Line)	25	159	1.83	0.014
Line	1	25.06	14.35	0.0008
Host \times Line	2	159	2.36	0.098
Host \times Family (Line)	50	159	1.14	0.27
r^2	0.57			

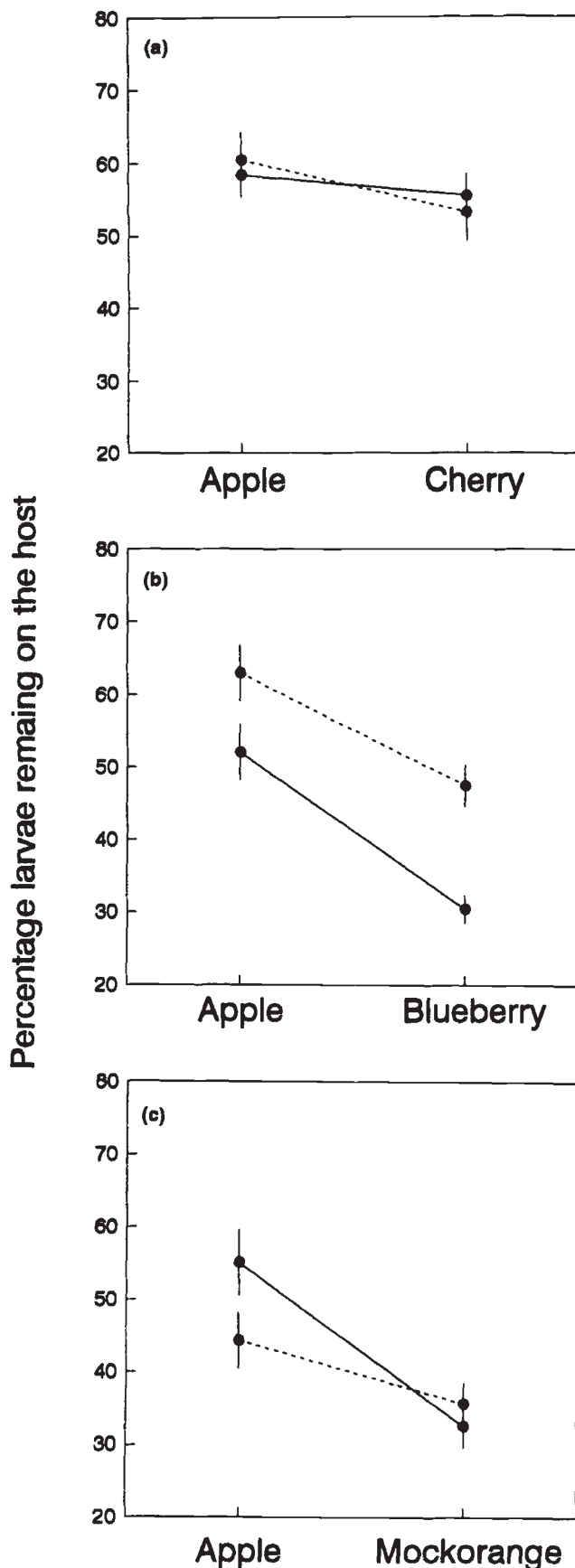
$N_{d.f.}$ and $D_{d.f.}$ are, respectively, the numerator and denominator degrees of freedom used in the Satterthwaite approximations of the F -tests (SAS Institute, 1988). r^2 measures how much variation in the dependent variable is accounted for by the model.

Table 6 ANOVAs to compare variation in larval host acceptance in three pairs of populations of the obliquebanded leafroller confined to habitats that differed in host species composition

Source	Apple-Cherry				Apple-Blueberry				Apple-Mockorange			
	$N_{d.f.}$	$D_{d.f.}$	F	P	$N_{d.f.}$	$D_{d.f.}$	F	P	$N_{d.f.}$	$D_{d.f.}$	F	P
Pop	1	6.59	0.002	0.96	1	3.16	14.22	0.030	1	1.14	0.53	0.59
Family (Pop)	21	21	2.47	0.022	19	19.32	1.85	0.093	16	16	2.26	0.057
Host	1	1	5.37	0.26	1	1	46.82	0.092	1	1	2.52	0.36
Pop \times Host	1	21.41	0.50	0.48	1	18.74	0.95	0.34	1	16	18.11	0.0006
Family (Pop) \times Host	21	178	1.41	0.12	18	114	1.09	0.37	16	144	1.38	0.16
r^2	0.37				0.54				0.55			

r^2 measures how much variation in the dependent variable is accounted for by the model.

$N_{d.f.}$ and $D_{d.f.}$ are, respectively, the numerator and denominator degrees of freedom used in the Satterthwaite approximations of the F -tests (SAS Institute, 1988).



In this study, we demonstrated that genetically based variation in larval host acceptance was present within populations of *C. rosaceana*. The comparisons of pairs of populations, and the indirect responses to selection on host-acceptance behaviour, provide evidence that the genetic correlations between acceptance of different host species were either positive or not significantly different from zero. The data also suggest that the norms of reaction for host response differed in two pairs of allopatric populations, but were similar between two populations assumed to be sympatric (Fig. 2). We discuss below the implication of these findings on the evolution of diet in *C. rosaceana* and in other plant-feeding insects.

Heritability of host acceptance

Values of heritability, and the outcome of selection experiments, always depend on the environment in which the experiments are made and on the populations studied (Falconer, 1981; Via, 1990). The reliability of the bioassay to reproduce field conditions (Carrière, 1992c), the repeated significance of the family effect in different populations, and the results of the selection experiment suggest, however, that there was additive genetic variance in host-selection behaviour within field populations of *C. rosaceana*.

Heritable variation in host-selection behaviour has often been found within populations of adult herbivorous insects. Such variation is apparently common for oviposition preference (reviewed in Via, 1990; Jaenike & Holt, 1991; Thompson & Pellmyr, 1991). Populations of aphids can show genetically based differences in their tendency to migrate from (Lamb & Mackay, 1979; Groeters, 1989), or move between (Bell, 1991) their hosts. Dispersal tendency (host acceptance) was shown to respond rapidly to selection in a polyphagous mite species (Fry, 1989; Li & Margolies, 1994). Few investigations, however, have reported evidence for genetically determined differences in larval host-selection behaviour. The tendency to settle on different algal species differed genetically both within and among populations in larvae of a marine polychaete (Mackay & Doyle, 1978). Heritable variation in food/habitat choice (Wallin, 1988; reviewed in Bell, 1991) and posi-

Fig. 2 Comparison of the average host acceptance ($\% \pm \text{SE}$) between populations of *Choristoneura rosaceana* collected in different habitats. (a) Populations assumed to be sympatric and collected from apple (solid line) or cherry orchards (broken line). (b) Allopatric populations collected from an apple orchard (solid line) or a blueberry field (broken line). (c) Allopatric populations collected from an apple orchard (solid line) or a mixed forest (broken line).

tive genetic correlation between habitat choice and development rate (Taylor & Condra, 1983) were found in *Drosophila* larvae.

Genetic correlations between host responses

The differences in response to the apple and rose hosts between the selected lines suggest that positive genetic correlations between host responses were present within the selected population. In the comparisons of pairs of populations, only one of the five genetic correlations in acceptance of the host-pairs was significant, but the correlation coefficients were always positive with an average value of 0.41 ± 0.07 (\pm SE). Therefore, there is no evidence that negative genetic correlations between the responses to different host species were present in populations of *C. rosaceana*. Such a genetic architecture of host-selection behaviour implies that selection for increased acceptance of a particular host would not result in any loss of ability to accept another host, which could favour polyphagy in this leafroller.

Few studies have attempted to measure genetic correlations between the responses to hosts (Arnold, 1981; Wasserman, 1986; Courtney & Hard, 1990), and a genetic trade-off in host response was only found in the anise swallowtail butterfly, *Papilio zelicaon* (Thompson, 1993). In that species, a negative genetic correlation between oviposition preference for fennel (*Foeniculum vulgare*) and *Cymopterus terebinthinus* was found in a population of ecological specialists on fennel. After escaping from cultivation, fennel was incorporated into the diet of *P. zelicaon* as a low-ranking host (Thompson, 1993). *Cymopterus terebinthinus*, however, is a high-ranking native host. Therefore, it can be predicted that a selective increase in preference for fennel in the monophagous population should result in a correlated decrease in preference for *Cymopterus terebinthinus*. A comparison of host-selection behaviour between the monophagous population and a population that exploited *Cymopterus terebinthinus* and another native host suggests that this prediction was realized (see Thompson, 1993, table 1). Despite the detection of such a negative genetic correlation in oviposition preference, it is remarkable that the rank-order of host preference appeared to be evolutionarily conservative across the swallowtail populations studied by Thompson (1993).

In the highly specialized *Lapeyresia pomonella*, however, it is clear that the evolution of increased oviposition preference for a novel host, which was initially ranked lower than the ancestral host, resulted in a change in the rank-order of host preference (Phillips & Barnes, 1975). The *L. pomonella* populations were exploiting different monocultures and became special-

ists on dissimilar hosts. This is in opposition to the predictions of the hierarchy threshold model (Courtney *et al.*, 1989; Courtney & Hard, 1990), which proposes that the rank-order of host preference in insect herbivores is evolutionarily conservative. Therefore, such a model is not allowing for the existence of strong negative genetic correlations between the tendencies to accept different hosts. The rapidity of these behavioural changes (taking place in less than 100 years), and the fact that preference for the ancestral host always declined following increased acceptance of the novel host, suggest that the divergences in behaviour were not simply because of the effect of genetic drift. Therefore, negative genetic correlations between acceptances of different hosts may play a major role in shaping diet in *L. pomonella*. Further studies are needed to assess the frequency of negative genetic correlations between responses to different hosts in plant-feeding insects.

Comparison of norms of reaction in pairs of populations

Optimal foraging models suggest that costs associated with host discrimination (e.g. reduction in realized fecundity, mortality due to dispersal) may be balanced by the benefit of locating highly suitable resources (Roitberg & Mangel, 1993 and references therein). In reproductively isolated populations remaining in association with monocultures, however, the cultivated crop is virtually the only host present, and increased acceptance of the cultivated crop could be favoured. Such a modification in host-selection behaviour would be more likely to occur if a low-ranking host is colonized, since a low-ranking host could be strongly rejected initially but eventually accepted, thereby creating an opportunity for selection to decrease the length of the discrimination phase (see Wiklund, 1981; Singer, 1986).

The comparison between the Apple and Mixed forest populations (Fig. 2c) supports the hypothesis that an increase in host acceptance is favoured in monocultures. A similar phenomenon was observed in *L. pomonella* (Phillips & Barnes, 1975) and in *Liriomyza brassica* (Tavormina, 1982). In the Blueberry population, however, larvae had a higher acceptance of the blueberry and apple hosts than individuals from the Apple population (Fig. 2b). Such a divergence in host-selection behaviour may result from two, non-exclusive factors: (i) a selective increase in blueberry acceptance in the Blueberry population may have resulted in a correlated increase in apple acceptance, and (ii) low host acceptance may have been present in the Apple population. Nevertheless, no strongly 'cross-

ing' norms of reactions were observed in the pairs of allopatric populations. This corroborates the previous statement that the evolution of high acceptance of a specific host should favour polyphagy in *C. rosaceana*.

It seems reasonable to infer that local changes in host species' composition gave rise to between-population variation in larval host-selection behaviour. Inter-habitat variation in other ecological factors, however, may have also influenced host-selection behaviour (Jaenike, 1990; Johnson & Gaines, 1990). For example, across-habitat variation in mortality risk associated with larval dispersal may have favoured local changes in host acceptance. Finally, founder effects arising because the blueberry and mixed forest colonies were established from small field-collected samples may have contributed to the between-population differences in host-selection behaviour.

Researchers studying the evolution of diet breadth in insect herbivores have concentrated on life history characters expressed on different hosts. The scale at which independently evolving units differ in such host-use traits varies considerably among insect species. It ranges from individual plants (Karban, 1989), adjacent patches, fields or forest stands (Mitter *et al.*, 1979; Schneider, 1980; Thompson, 1985; Via, 1991), to regions corresponding to allopatric sets of plant species (Scriber, 1988; Hagen, 1990). The present study suggests that local variation in host species' frequency has influenced the evolution of host-selection behaviour in *C. rosaceana*. Recent reviews of the literature (Courtney *et al.*, 1989; Jaenike & Holt, 1991; Carrière & Roitberg, unpublished observations), as well as the results of this study, suggest that such an evolutionary change in host selection behaviour is generally not accompanied by behavioural specialization in plant-feeding insects.

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