ECOLOGICAL GENETICS OF HOST EXPLOITATION IN A GENERALIST HERBIVORE, THE OBLIQUEBANDED LEAFROLLER

by

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ECOLOGICAL GENETICS OF HOST EXPLOITATION IN A GENERALIST HERBIVORE,

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ABSTRACT

Generalist herbivorous insects may function as specialists who adopt a locally restricted diet breadth. Evolutionary change in host exploitation traits could be one mechanism leading to ecological specialization. I used an ecological genetic approach to investigate the evolution of larval life-history traits and host-selection behavior in a polyphagous insect, the obliquebanded leafroller (OBL), *Choristoneura rosaceana* (Harris), a pest of fruit crops in the Okanagan Valley, B.C.

The feeding performance of a population that had been exploiting an apple orchard for at least 10 generations was studied in the laboratory. Insects attained a higher pupal size when feeding on apple leaves than when feeding on three native host species. A positive correlation between pupal size and female fecundity was found in the field. The high suitability of apple and its abundance in the valley would facilitate the evolution of a strong preference for that crop in the OBL.

The comparison of feeding performance of individual families on host-pairs revealed that genetic variation in feeding specialization on apple was present in this population. Feeding trade-offs on host-pairs (negative full-sib genetic correlations) were also found after correcting statistically for the potential impact of general vigor and/or maternal effects. These findings support the hypothesis that

feeding trade-offs favor the evolution of specialization in phytophagous insects.

In an independent experiment, maternal effects influenced the mean phenotype, variance, and heritability of many feeding performance traits. This suggests that the statistical corrections of the full-sib genetic correlations in feeding performance corrected for maternal effects.

Newly emerged larvae exhibited different dispersal rates from four host species. Significant genetic variation in larval host selection (host-specific dispersal rates) was found within two populations. Genetically-based variation in host-specific dispersal rates was also found among populations, and supported the hypothesis that high searching costs favor the evolution of polyphagy.

This thesis suggests that evolutionary changes in host exploitation traits may be a significant mechanism leading to ecological specialization in the OBL.

DEDICATION

A Réjane, Jacques,

Benoit, Denis et Dominique,

avec toute mon affection.

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GENERAL INTRODUCTION

The evolution of diet breadth in phytophagous insects provides information for testing hypotheses of ecological specialization and sympatric speciation (Rausher 1984, Futuyma and Peterson, 1985, Tauber and Tauber, 1989). Studies of diet breadth may also contribute to the development of strategies for pest management, by providing information on 1) pest evolution in reaction to agricultural management, 2) host shifts, and 3) "host race" formation (Diehl and Bush, 1984, Gould, 1988, Via, 1990).

While adaptive changes in insects' diets are guided by natural selection, genetic constraints on the ability of herbivores to efficiently use plant species differing in chemical constitution, or to discriminate among many hosts, was proposed to influence host range (Dethier, 1954, Levins and MacArthur, 1969, Futuyma, 1983, Rausher, 1991). In addition, many ecological factors affect host specialization and a multi-factorial approach should be favored to uncover the relationship between such factors and evolutionary changes in host use by herbivores (Barbosa, 1988, Jaenike, 1990). Therefore, three complementary approaches may be used to understand the evolution of insect/plant interactions: ecological studies can be used to identify the selective factors that influence host use, evolutionary theories of behavior may guide tests of complex hypotheses,

and the concepts and methods of ecological genetics are appropriate to understand the responses to selection (Thompson, 1988, Via, 1990).

Population and quantitative genetic models are useful in understanding the course of adaptive changes in characters of ecological importance to herbivorous insects (Via, 1990). When continuously varying quantitative characters are studied, these models require the measurement of two basic parameters. First, the evolutionary potential of characters within specific populations can be estimated, by measuring the proportion of additive genetic variation in, and the pattern of genetic covariation among these characters. Estimation of genetic variation and covariation also permits the evaluation of hypotheses that rely on particular genetic structures, such as the hypothesis that trade-offs in feeding performance on different hosts are present within insect populations (Rausher, 1984, Via, 1984). Second, measurements of the intensity of natural selection through changes in the distribution of the phenotypic characters are needed to formulate quantitative predictions of evolutionary changes (Lande and Arnold, 1983, Wade and Kalisz, 1990). However, even though several studies of phytophagous insects have detected natural selection operating on host-use traits (e.g. Tabashnik, 1983, Karban, 1989, Via, 1991), formal estimates of the intensity of natural selection on life-history characters or host-selection behavior have not been done (Via, 1990).

Recent studies have shown that colonization of new habitats may affect differently the relationship between host preference and performance in insect species (or populations). In some species, populations exploiting different habitats diverged exclusively in host feeding performance (e.g. Tabashnick, 1983), or in host preference (e.g. Futuyma et al., 1984, Thomas et al., 1987). Yet, in other populations, positive correlations between preference and performance were found, suggesting that both traits were correlated genetically and that they had the potential to covary (Via, 1986, Singer et al., 1988). Such variation in population responses to habitat changes are difficult to understand, without a measure of the genetic variation and covariation of the characters related to host use, and of the intensity of selection that operates on host preference and performance. Therefore, the methods of ecological genetics constitute a powerful tool to explore the complex evolutionary mechanisms involved in host shifts in phytophagous insects.

The study of diet breadth should concentrate on assessing the relative role of diverse evolutionary pressures in favoring the evolution of particular host ranges. A global understanding of host-range evolution will depend on our ability to correlate inter-population or inter-specific variation in diet breadth to specific aspects of the insects' genetic system (Jaenike, 1986, Via, 1986, Singer et al., 1989, Thompson et al., 1990), ecology

(Bernays and Graham, 1988, Smith, 1988, Thompson, 1988, Wood and Keese, 1990), physiology (Futuyma and Philippi, 1987, Karowe, 1989), life-history (Courtney and Hard, 1990) and behavior (Singer, 1983, Jaenike, 1985, Thomas and Singer, 1987).

This thesis examines the ecological genetics of host exploitation in a generalist herbivore, the obliquebanded leafroller (OBL), *Choristoneura rosaceana* (Harris). This polyphagous tortricid feeds on a variety of deciduous trees and shrubs. In the Okanagan Valley of British Columbia, where this research was conducted, the OBL is a pest of apple and cherry crops. The OBL selects hosts in two ways: the females fly and lay egg batches on host leaves, and newly hatched larvae may contact various host species after dispersing on silk threads. Although larval dispersal results essentially in random intra-habitat movements, the larvae have the ability to select hosts by accepting or rejecting them once encountered. A general objective of the thesis is to estimate the evolutionary potential of larval life history traits and host preference with respect to changes in the mix of hosts available in the insect's habitat. A second objective is to use the OBL as a model to test current hypotheses on the evolution of host preference in phytophagous insects.

The thesis begins with an estimate of larval feeding performance on apple leaves and three alternative hosts commonly used by this species (Chapter 2). The estimates

are made to facilitate development of qualitative predictions on the evolution of host use in the obliquebanded leafroller. Some proximal factors affecting larval dispersal are studied in Chapter 3, to provide the basic information necessary to investigate the evolution of larval host preference. In Chapter 4, the hypothesis that feeding trade-offs are present in the OBL is tested. The presence of feeding trade-offs is thought to be an important factor favoring the evolution of specialization in host-selection behavior. Chapter 5 extends the work undertaken in Chapter 4. It includes a detailed investigation of maternal effects as a source of variation in life-history traits. Chapter 6 is a test of the hypothesis that high searching costs favor the evolution of broad host acceptance. Host-selection behavior is compared among populations exploiting different habitats to investigate whether the larvae evolve a preference for locally abundant hosts, and whether the changes in larval host responses effectively result in an expanded range of host acceptance. Finally, Chapter 7 summarizes the results of the previous chapters.

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Chapter 2:
HOST PLANT EXPLOITATION WITHIN A POPULATION OF THE OBLIQUEBANDED LEAFROLLER

SUMMARY

Feeding performance of larvae of the obliquebanded leafroller, *Choristoneura rosaceana*, was estimated on apple and three alternative hosts in the Okanagan Valley. The obliquebanded leafroller is native to the study area and apple was introduced in the valley at the beginning of the century. Components of insect fitness were measured to help formulate predictions about the evolution of host preference in this generalist herbivore. In the summer, pupal weight was influenced by diet; females attained a higher pupal weight on apple than on trembling aspen, wild rose and snowberry. Males performed best on apple and trembling aspen. In the field, females arising from caterpillars fed apple leaves had a 26% greater mean fecundity than if fed alternative hosts. The diet also effected development time; females initiated pupation later on trembling aspen than on the other hosts. Finally, no differences were found in larval survival, or in the proportion of larvae diapausing when fed on different hosts. These components of fitness indicate apple as the most suitable host in the summer.

In the fall, diet influenced larval propensity to initiate diapause in the second or third instar, the time elapsed from hatching to diapause initiation and the weight of the instars initiating diapause. However, no difference in overwintering survival among larvae fed on different hosts was detected. The rank order of water and nitrogen contents of leaves of the host plants did not match the rank order of larval feeding performance in either season. A high suitability of apple and its abundance in the Okanagan Valley are factors that would favor the evolution of an increased utilization of this host by the obliquebanded leafroller.

INTRODUCTION

Generalist insects colonize introduced plant species at a faster rate than do specialists, which suggests that they are pre-adapted to incorporate new hosts into their diet (Strong et al., 1984). Even if polyphagous insects are flexible in exploiting hosts, a differential use of the plant species available in their foraging space can have fitness consequences (Otte and Joern, 1977, Lance, 1983, Via, 1984). Thus, colonization of new areas, perturbations of the insect environment, or heterogeneity in the habitat, may favor evolutionary changes in host-selection behaviors and/or performance traits (Fox and Morrow, 1981, Thomas et al., 1987, Gould, 1988, Chapter 6).

Optimal foraging (Jaenike, 1978, Courtney, 1982, Ward, 1987) and population genetic or mathematical models (Gould, 1984, Castillo-Chavez et al., 1988) suggest that host relative suitability and availability (determined by the insects' ability to move and locate different resources; Wiklund, 1982), are important factors influencing the evolution of host preference in phytophagous insects. Given that 1) fitness on a novel host exeeds fitness on other hosts, and 2) there is expressed genetic variation for host preference and no unfavorable genetic correlations in performance across existing hosts, it can be anticipated that selection will act to increase preference for a novel host (Karowe, 1990). Thus, estimates of relative feeding

performance of an insect herbivore on its potential hosts can provide valuable information on how its diet will change over evolutionary time. However, other factors undoubtedly determine the hosts' relative overall suitability (Thompson, 1988, Jaenike, 1990) and could limit the power of such predictions.

The obliquebanded leafroller (OBL), *Choristoneura rosaceana* (Harris), is a polyphagous tortricid native of North America, which can use a variety of deciduous trees, shrubs and even conifers as hosts (Chapman and Lienk, 1971). During the last century, the bunch grass-ponderosa pine habitat typical of the Okanagan Valley in British Columbia, Canada, was replaced by commercial orchards. Subsequently, the OBL has become a pest of fruit crops, because the larvae can tie leaves to fruits when building leafrolls and subsequently damage the fruit surface (Aliniazee, 1986). The OBL can select hosts in two ways: 1) females fly and lay eggs in batches on the upper surface of host-leaves, and 2) newly hatched larvae may balloon with the aid of silk threads to locate new hosts (Chapman and Lienk, 1971).

Moths are bi-voltine in the Okanagan Valley and larvae use hosts throughout the summer. It is known that variation in the concentrations of plant nutritive elements are correlated with insect feeding performances (Mattson and Scriber, 1988). Water and nitrogen content are good predictors of insect growth on different plant species; they generally decrease at a slower rate and remain higher in

bushes than in trees during the growing season (Scriber, 1984). Thus, the relative reproductive success of OBL larvae using bushes or trees might change seasonally with concentration of nutrients.

The objective of this study was to estimate components of feeding performance for both generations of the OBL on apple and on three alternative hosts. Two tree and two bush species were chosen as hosts to determine whether differential changes in plant quality over the growing season could result in changes in the rank order of host suitability. This information was collected to help formulate predictions about the evolution of host preference in the OBL.

METHODS AND MATERIALS

Feeding performance of caterpillars was measured in two experiments conducted in the laboratory between June 15 and August 18, 1989 and between August 25 and September 14, 1988. These will be referred to as the summer and fall experiments, respectively. Both experiments were conducted in a walk-in growth chamber at 25 °C under a 16L:8D photoperiod (summer) and at 20 °C under a 14L:10D photoperiod (fall).

Larvae hatching from the females' first egg mass were used. Experiments were begun approximately two weeks after the onset of adult emergence in the field. The onset of the first and the second adult flights was determined with the

aid of pheromone traps and the observed adult emergence times for insects reared in the field, respectively.

Origin of the insects. The insects used in this experiment were all collected from a single apple orchard at Winfield, B.C. In this area, OBL larvae were found only in three adjacent apple orchards and in two cherry blocks. They were infrequently discovered on other plant species.

Larvae used in the fall experiment originated from the second generation of adults in my laboratory colony (see Chapter 3). The summer experiment was conducted using larvae produced by females which developed from field collected 5- and 6-th instar larvae. To obtain adults, field collected larvae were fed individually until pupation in petri dishes on excised apple leaves (leaves were replaced every second day).

Origin of the host plants. The four hosts were collected at the Agriculture Canada Summerland Research Station. Two tree and two bush species were used in the feeding experiments: Red Delicious apple cultivar(*Malus domestica;* A), trembling aspen (*Populus tremeloides;* TA), wild rose (*Rosa* sp.; R) and snowberry (*Shepherdia canadensis;* S). At Summerland, OBL larvae had occasionally been found in the field on all the alternative hosts .

The A branches used were extension shoots (producing leaves continuously) collected from a block of trees which

was ca. 25 years old. Except for an early spring pesticide treatment in the first week of May, the A trees were not sprayed with any chemicals during the experimental years. The R branches were "long shoots" (i.e. with continuous flushing), the S branches were a mixture of "long" and "short" shoots ("short shoots" produce leaves in a synchronous flush) and the TA branches were "short" shoots. To minimize among-habitat differences in plant quality, the branches employed for the summer and fall tests were collected in the same apple block and R, S and TA patches.

For each plant species, terminal shoots (ca. 20 cm long) were divided into sections with 2-3 leaves (composite leaves for R, groups of opposite leaves for S) or one leaf cluster for TA. The cut end of the branches were immediately immersed in water and taken into the laboratory. If present, fruits were removed from branch segments before being offered to larvae.

Insect feeding procedure

a) Summer experiment

The goal of this experiment was to estimate components of fitness on the four hosts; larval mortality, total development time and pupal weight were measured. Insects were reared in 650 ml clear plastic cages. Two sprigs of each host, inserted in a plastic vial filled with water and fitted with a rubber cap, were inserted through the bottom of each cage. Plant material was replaced every third day.

Preliminary experiments demonstrated that the initial water content of the plants was maintained for three days under the experimental conditions used.

Eleven arbitrarily selected mating pairs produced the larvae used in this experiment. Forty larvae per pair were reared on each host, at an initial density of four hatchlings per cage. When the plants were replaced, larval mortality was noted and the larvae were redistributed in equal densities across the 10 feeding cages used to feed a family group on each host plant. Throughout the experiment, at least half of the leaves were still present at the end of the feeding periods in each cage. Each family group raised on a host was randomly assigned to one section of the growth chamber. Every day, all groups were randomly relocated to minimize potential microclimatic effects on insect growth.

After 18 days, some larvae (which were much smaller than the rest of the larvae) were found crawling in the cages, apparently searching for a diapausing site. This suggested that diapausing propensities may vary among hosts. All larvae were weighed at that time and the smaller larvae, weighing less than 3.5 mg, were either 1) transferred individually to plastic cups containing a piece of cardboard as a diapausing site, 2) discarded, or 3) fed to determine whether they would eventually complete development. The 3.5 mg limit was chosen arbitrarily. Plastic cups were maintained in the same growth chamber used to raise the insects and they were checked 2-3 weeks later for the

presence of diapausing cocoons. All larvae weighing more than 3.5 mg were fed until pupation and pupae were weighed on the day they were found.

Total developmental time was recorded in multiples of three days. Consequently, the effect of host species on development time was analyzed using a three way log-linear model (LLM) appropriate for categorical data (Host, Sex and Development time were the "main" effects). The program BMDP4F (BMDP Institute, 1990) was used to investigate the nature of the significance of second order effects (this is analogous to conducting *a posteriori* tests among levels of a treatment in an ANOVA). To do this, the hierarchical LLM that was found to represent the structure of the data was fitted, without the second order effect of interest. Cells that were most likely to be responsible for the lack of fit to this incomplete model were located (by finding the cells with the largest Freeman-Tukey deviates). The significance of the contribution of each of these cells to the incomplete model was then estimated, after they had been deleted from the model in a stepwise manner.

b) Fall experiment

As in the summer experiment, this phase of the study was conducted to estimate components of fitness on the four hosts. The time elapsed from hatching to diapause initiation and overwintering survival were estimated for larvae originating from 12 families. Twenty-four larvae per family were fed on each host at an initial density of three

larvae per cage. The feeding procedure was the same as in the summer experiment, except that smaller cages (150 ml), with openings covered with fine nylon mesh, were used. Some of the hatchlings were able to escape through the mesh in the first days of the experiment and therefore larval mortality could not be recorded.

Every third day, larvae found crawling in the cages were weighed and transferred to plastic cups, as described previously, and the time spent from feeding initiation to onset of crawling was noted. Some larvae spun cocoons directly in the cages and were included to estimate the proportion of larvae initiating diapause on each host.

The effects of host plant species on the weight of wandering larvae and on the relationship between larval weight and overwintering survival were analysed using a one-way and a two-way ANOVA, respectively. Larval weight was transformed (using a technique outlined in Wright 1968, Chapt. 10) to meet the conditions of normality and homogeneity of variance.

Survival of the diapausing larvae in the field. To quantify host-specific overwintering survival, the diapausing larvae were placed in an outdoor insectary three weeks after being transferred to plastic cups. Summer and fall larvae were kept in plastic trays and inside a cardboard box lined with newsprint, respectively. Larval survival was assessed the following spring at the end of April, May and June.

Surviving larvae were easy to recognize; their cocoons had been perforated when they emerged from diapause.

Relationship between female pupal weight and total fecundity in the field. The relationship between pupal weight and total fecundity may not be as general as previously proposed (Leather, 1988). To estimate this relationship in the OBL, newly emerged females from the summer feeding experiment were caged individually in an outdoor insectary with a newly emerged male and allowed to mate overnight. The following morning, couples were transferred to 300 ml cages containing water and waxed paper (as an oviposition site). For each female, the contours of all egg masses were traced on transparency acetate. After being magnified, the surface of the egg masses were estimated (in cm^2) using an Apple graphics tablet digitizing pad.

The lifetime fecundity of females was calculated by transforming the area of the females' egg masses to egg counts using a previously established relationship between egg mass area and egg number per mass. This relationship was obtained for egg masses laid on 1) wax paper by colony raised insects, and 2) leaf surfaces by females originating from field collected larvae fed on apple leaves. Egg mass area and egg counts were square root transformed before being regressed to meet the assumption of homogeneity of variance in the residuals across different values of X. The relationships between egg mass areas and the number of eggs

they contained were SQR (EGGS) = 29.845 (SQR [AREA]) - 1.745, $F_{1,57}$ = 381.105, r^2 = 0.87, P < 0.0001 and SQR (EGGS) = 29.229 (SQR [AREA]) - 1.502, $F_{1,37}$ = 688.715, r^2 = 0.95, P < 0.0001 for egg masses laid on leaves and on wax paper, respectively. The slopes of these linear relationships were not statistically different (ANCOVA, Substratum * Surface effect, $F_{1,94}$ = 0.106, P = 0.746). The substratum on which the females laid had no significant effect on the number of eggs packed in an egg mass of a given size (ANCOVA, Substratum effect, $F_{1,95}$ = 0.178, P = 0.674). Consequently, both data sets were pooled to yield the relationship SQR (EGGS) = 29.369 (SQR [AREA]) - 1.527, $F_{1,96}$ = 1101.060, r^2 = 0.92, P < 0.0001, which was used to estimate the number of eggs contained in egg masses obtained in the oviposition experiment.

Females used in the experiment to establish the relationship between female pupal weight and lifetime fecundity had been reared on one of four hosts. A covariance analysis was used to determine whether the host on which females had fed could affect their total fecundity for a given pupal weight. Host was the fixed effect and female pupal weight the covariate. Some OBL females resumed their calling behavior following oviposition of their first egg mass. Such females need a second mating to lay their full complement of eggs (Carrière, unpubl. data). Because it seemed that males found it difficult to locate a calling female and to mate a second time in the experimental cages,

only females which had laid at least two egg masses were included in the analysis.

In all ANOVAs, type 3 sums of squares were used for significance tests (SAS Institute, 1985). All LLMs were fitted using the CATMOD package in SAS, except when stepwise identification of cells deviates were performed.

RESULTS

Summer feeding experiment. The small larvae transferred to plastic cups for diapause induction were observed either crawling in the cages or hiding/feeding on the plants. Sixty-two percent of the larvae transferred (n = 180) spun a cocoon and diapaused. These larvae were all third instars (except one second instar found on A) and did not differ significantly in size with respect to the host plant on which they were raised (one way ANOVA on ln transformed larval weight; $F_{3,108} = 1.232$, $P = 0.302$; see Table 2.1).

Larvae that successfully diapaused after their transfer (1.1 ± 0.5 mg, [Mean ± s.d.] Range 0.3 - 3.5 mg) were smaller than larvae which failed to diapause (1.5 ± 0.7mg, Range 0.4 - 3.5 mg) ($t = - 3.253$, $df = 110$, $P = 0.002$; t-test performed on ln transformed larval weights). Some of the larvae weighing less than 3.5 mg which were fed apple leaves successfully pupated, although their total developmental time was apparently longer than larvae which weighed > 3.5 mg on day 18 (four males and three females fed

on apple completed development, with an average developmental time of 31 and 34 days respectively; see Table 2.3 for developmental times of > 3.5 mg larvae).

It was not possible to estimate directly the proportion of diapausing caterpillars on each host because only a subset of the small larvae were transferred to diapausing cups. Consequently, all larvae weighing less than 1.1 mg after 18 days (the mean size at which the transferred larvae successfully diapaused) were scored as diapausing larvae. Using this estimate of diapausing state, no significant difference in the proportion of larvae that diapaused when fed on different host plants was found (one way ANOVA on arcsin transformed proportions of diapausing larvae in each family; $F_{3,40} = 0.73$, $P = 0.5414$; see Table 2.1).

No statistical difference in larval mortality on the four hosts was found from day 0 to 18 (one way ANOVA on arcsin transformed proportions of mortality in each family; $F_{3,40} = 0.639$, $P = 0.595$) or from day 18 to pupation (one way ANOVA on arcsin transformed proportions of mortality in each family; $F_{3,39} = 0.548$, $P = 0.652$; see Table 2.2).

The saturated LLM describing the larval development time data fitted well (Host X Sex X Development time effect; $X^2 = 17.67$, df = 15, $P = 0.2804$). Significant terms in the model included Development time ($X^2 = 77.11$, df = 5, $P = 0.0001$), Host X Development time ($X^2 = 27.19$, df = 15, $P = 0.0273$) and Sex X Development time ($X^2 = 29.23$, df =

Table 2.1: Mean proportion of larvae entering diapause after 18 days of feeding among 11 OBL families fed four different host species in the summer

Host[1]	% Diapause (Mean ± s.d.)	Weight (mg) of transferred larvae (Mean ± s.d.)
A	23 ± 16	1.4 ± 0.7 (n = 37)
TA	24 ± 21	1.2 ± 0.6 (n = 46)
R	22 ± 24	1.1 ± 0.8 (n = 17)
S	13 ± 13	1.2 ± 0.6 (n = 12)

[1] A= apple, TA= trembling aspen, R= rose, S= snowberry.

Table 2.2: Mean mortality among OBL larvae originating from 11 families fed on four different host species in the summer from the onset of feeding to day 18, or day 18 to pupation

Host[1]	Mortality 0-18 (± s.d.)	Mortality 18-Pupae (± s.d.)2
A	0.65 ± 0.10	0.11 ± 0.13
TA	0.58 ± 0.12	0.08 ± 0.11
R	0.62 ± 0.10	0.05 ± 0.07
S	0.63 ± 0.08	0.09 ± 0.09

1 A= apple, TA= trembling aspen, R= rose, S= snowberry.

2 Mortality from day 18 to pupation estimated for larvae > 3.5 mg only.

Table 2.3: Mean development time for male and female OBL larvae feeding on four different host species in the summer

Host[1]	Development time (days)[2]			
	Male	n	Female	n
A	27	49	29	40
TA	28	46	30	58
R	26	60	28	50
S	27	49	29	69

1 A= apple, TA= trembling aspen, R= rose, S= snowberry.

2 No standard errors are presented because mean development times were calculated from data obtained from cencus taken every third day.

15, P = 0.0001). This indicates that the distribution of development times was dependent upon Sex and Host (see Table 2.3).

The stepwise procedure showed that the significant Sex X Development time effect was due to four cells. The incomplete model including only the Development time and Host X Development time effects fitted the data well, when cells corresponding to males in the most rapid developmental category (<21 d) on A, R and S, and to males in the second fastest developmental category (<24 d) on TA, were excluded. Contrary to males, only one female had completed development in less than 21 d (on R), and after 24 d, only one female pupa had been found on TA. Thus, the dependance of the distribution of development times on Sex was mainly due to the fact that males could initiate pupation earlier than females on the four hosts. The stepwise procedure also showed that the significant Host X Development time effect was only due to one cell; relatively few female pupae had been found on day 24 on TA. This suggests that the distribution of development times was similar on all hosts except on TA, because females could not initiate pupation as fast on TA as on the other hosts.

Females attained a larger pupal size than males (two way ANOVA, $F_{1,413} = 712.34$, P = 0.0001; see Table 2.4). Averaged over sex, there was also a significant difference in mean pupating size on the four hosts ($F_{3,413} = 27.44$, P = 0.0001). The difference in mean pupal weight between males

and females varied with respect to the host, as indicated by the significant interaction term (Host X Sex effect; $F_{3,413}$ = 6.90, P = 0.0002). Males attained a greater pupal size on trees than bushes and females performed best on A (Table 2.4).

Fall feeding experiment. At least 74% of the larvae raised on each host successfully diapaused after being transferred to diapausing cups (76, 76, 74 and 80 % on A, R, S and TA respectively). The proportion of larvae initiating diapause in the second or third instar differed in larvae fed on different hosts (Host X Instar effect, X^2 = 50.52, df = 3, P = 0.0001; Table 2.5). Host type influenced the distribution of the time at which second instar larvae started wandering (Host X Time effect, X^2 = 16.37, df = 6, P = 0.012), but did not have such an effect on third instars (Host X Time effect, df = 6, P = 0.301). The average time at which larvae fed on A, R, S and TA started wandering was 9.7, 9.5, 10.1 and 10.3 days for second instars and 13.2, 13.9, 13.4 and 13.9 days for third instars, respectively.

A significant difference in the mean weight of the wandering larvae fed on different hosts was found when the second and third larval instars were pooled for analysis (one way ANOVA on $\log_{10}$ (weight + 15.8) transformed data, $F_{3,457}$ = 12.335, P < 0.0001). Average weights of wandering larvae were the smallest on A and R, intermediate on S and the largest on TA (Tukey tests, P < 0.05). This was due to

Table 2.4: Mean pupal weight for male and female OBL attained on four host species in the summer

Host[1]	Pupal weight (mg ± s.d.)[2]	
	Male	Female
A	51 ± 9 a	91 ± 16 a
TA	49 ± 9 a	76 ± 16 b
R	45 ± 7 b	72 ± 12 b
S	44 ± 8 b	71 ± 12 b

1 A= apple, TA= trembling aspen, R= rose, S= snowberry.

2 Means within columns followed by the same letter are not significantly different, Tukey tests, $P < 0.05$.

Table 2.5: Proportion of OBL larvae initiating diapause in the second or third instar on four host species in the fall

Host[1]	Instar		Total number of diapausing larvae
	2nd	3rd [2]	
A	0.79	0.21 a	116
TA	0.48	0.52 b	165
R	0.80	0.20 a	123
S	0.54	0.46 b	130

[1] A= apple, TA= trembling aspen, R= rose, S= snowberry.

[2] Proportions of larvae initiating diapause in their third instar on each host species followed by the same letter are not significantly different, G-test for homogeneity of percentages, $P < 0.05$.

a rapid wandering initiation on A and R (Table 2.5) and also to differences in the weight at which second and third instar larvae initiated wandering when reared on different hosts (Host X Instar interaction term, $F_{3,457} = 7.069$, P = 0.0001; see Table 2.6).

Survival of the diapausing larvae in the field. Only three of the 112 larvae which had initiated diapause in the summer emerged the following spring. The mean size of the larvae surviving winter (1.5 ± 0.3 mg [Mean ± s.d.]) seemed to be larger than the average size of the larvae that had been transferred into the field in the previous summer (1.1 ± 0.5 mg).

In the fall, larvae initiating diapause in the third instar had a greater survival than larvae which cocooned in the second instar (Instar X Condition effect, $X^2 = 32.44$, df = 1, P = 0.001; see Table 2.7). However, no differences in survival were detected among larvae reared on different hosts (Host X Condition effect, $X^2 = 3.31$, df = 3, P = 0.3458), even though more larvae initiated diapause in the third instar on S and TA than on A and R (Host X instar effect, $X^2 = 38.06$, P = 0.0001; see Table 2.7). The saturated model fitted the data well (Host X Instar X Condition effect, $X^2 = 0.13$, df = 3, P = 0.9882).

When both larval instars were pooled together, it was apparent that larvae that survived the winter were larger when initiating diapause than larvae that died (two-way

Table 2.6: Mean weight (mg) of OBL larval instars attained on different host species in the fall

Host[1]	Instar (Mean ± s.d.) [2]	
	2nd	3rd
A	0.27 ± 0.05 ab	0.51 ± 0.08 a
TA	0.30 ± 0.06 b	0.66 ± 0.29 b
R	0.26 ± 0.05 a	0.46 ± 0.07 a
S	0.28 ± 0.05 ab	0.55 ± 0.13 ab

[1] A= apple, TA= trembling aspen, R= rose, S= snowberry.

[2] Means within columns followed by the same letter are not significantly different, Tukey tests, $P < 0.05$.

Table 2.7: Proportion of the OBL larvae initiating diapause in the fall on different host species that survived

Host[1]	2nd instar		3rd instar	
	%	n[2]	%	n
A	0.38	63	0.71	17
TA	0.41	54	0.75	65
R	0.37	71	0.67	15
S	0.29	41	0.63	43

1 A= apple, TA= trembling aspen, R= rose, S= snowberry.

2 Number of larvae transferred to the field.

ANOVA on $\log_{10}$ [weight + 15.8] transformed data, Condition effect, $F_{1,361} = 24.50$, $P < 0.0001$). The difference in larval weight between surviving and dying larvae was consistent across the four hosts (Host X Condition effect, $F_{3,361} = 0.79$, $P = 0.4983$).

Relation between pupal weight and fecundity in the field. The slopes of the relationships between pupal weight and lifetime fecundity for females fed on different hosts were similar (ANCOVA, Host effect, $F_{3,29} = 0.794$, $P = 0.507$; females' lifetime fecundities Ln transformed). Host had no significant effect on total fecundity when the difference in pupal weights attained on each host was taken into account (ANCOVA, Host effect, $F_{3,32} = 2.537$, $P = 0.074$). Therefore, data for females fed on different hosts were pooled and the relationship between female pupal weight and lifetime fecundity in the field was estimated: Ln (EGGS) = 0.020 (WEIGHT) + 5.139, $F_{1,35} = 71.424$, $r^2 = 0.671$, $P < 0.0001$. Using this relationship and the mean pupal weight attained on each host (see Table 2.4), the predicted mean lifetime fecundity of an average female fed on A, TA, R and S (with associated 95% confidence limits) was 1053 (978 - 1133), 780 (732 - 831), 720 (675 - 767) and 706 (662 - 752) eggs, respectively.

DISCUSSION

This study was conducted to investigate whether apple and three native hosts of the OBL differed in suitability within and between seasons. In the summer, larval feeding performance differed among the hosts, a result that was also found in other generalist insects (Barbosa et al., 1983, Wint, 1983). Based on pupal weight attained on the hosts, apple was the most suitable host for both sexes in the OBL. Males attained a similar size on trembling aspen, the other tree species on which feeding performance was measured, as on apple. Pupal weight was positively correlated with female fecundity and was a good indicator of fitness in the field (see below). The fitness advantage of achieving a high pupal weight in males is unknown in this species. The only other performance trait that differed among insects reared on the various hosts was development time; females did not initiate pupation as early on TA as on other hosts. In the absence of agricultural protective measures, the high suitability of apple and its abundance in the Okanagan Valley are factors that might facilitate the evolution of behavioral modifications, resulting in an increased use of this host in the OBL diet.

However, additional hypotheses need to be tested before concluding that apple is usually among the most suitable hosts for the OBL in the Okanagan Valley. First, the high performance on apple observed in this population may already be the product of local specialization. The leafrollers

were present in this orchard for at least 10 generations prior to measuring components of fitness in the summer. Since there was genetic variation in feeding performance in this population (Chapter 4 and 5), it is possible that a greater ability to utilize apple, compared to the alternative hosts, has evolved following genetic isolation of this population and its segregation to this crop. Experiments involving reciprocal transfers of populations exploiting different monocultures would permit the investigation of this possibility. Second, the suitability of the alternative hosts used to measure feeding performance have to be representative of the suitability of the potential hosts available to the OBL in the valley. Previous assessments of host range in the OBL indicate that plants belonging to the Rosacea and some forest trees, including the genera *Populus*, are among the most favored hosts of this tortricid (Chapman et al., 1968). Finally and perhaps most importantly, variation in suitability within each host species, as well as between patches of the same host species, must be smaller than variation in suitability between host species.

In the fall, the fitness components estimated were larval overwintering survival and time elapsed between hatching and diapause initiation on the four hosts. No overall differences in overwintering survival were detected for larvae fed on different hosts. A greater proportion of larvae feeding on A and R entered diapause in the second

instar than larvae feeding on S and TA. Second instar larvae also entered diapause sooner on A and R than on S and TA but no such differences were observed in third instar larvae. As long as survival values differ between diapausing and feeding larvae, an earlier diapause induction could have some fitness effects. However, it is not clear at this point whether these host-specific responses affect fitness in the OBL. The pooled weight of the larval instars initiating diapause was small on A and R, intermediate on S and large on TA. In addition, successful overwintering larvae were heavier, when initiating diapause in the fall, than larvae that died during the winter. This suggests that in the fall, S and TA are more suitable hosts than A and R. However, because no difference was detected in the overall larval survival on the various hosts, I conclude that no important differences exist in performance on the four hosts in the fall.

Relation between feeding performance and plant nutrient content. Estimates of water and nitrogen contents during the growing season were obtained for the four hosts (Chapter 3; Table 3.3). The observed OBL performances in the summer are not in qualitative agreement with the expected association to host water and nitrogen contents. R would be predicted to be a better host than was observed in this study. OBL growth is known to be influenced negatively by cyanogenic glycosides (Kaethler et al., 1982), which are

present in wild rose (Barbosa and Krischick, 1987). Thus, the presence of toxic allelochemicals might explain the difference between predicted and observed performance on R.

In the fall, overwintering larval mortality was similar on the four hosts, even though the hosts' water and nitrogen contents were different. Thus, plant nutrient content was not a good indicator of this fitness component. The hypothesis that seasonal variation in plant nutrient content would affect the rank order of host suitability could not be addressed because concentrations of nutrients in different hosts did not vary significantly between seasons (see Chapter 3; Table 3.3)

Diapausing tactics in the OBL. In the summer experiment, a proportion of the larvae left the plant in search of a diapausing site after feeding for some time. In nature, larvae overwinter under bud scales or fragments of the bark (Chapman and Lienk, 1971) and such a wandering period must occur. Some of the small larvae (<3.5 mg) at 18 days were able to complete development when not given access to a diapausing site, although their total development time seemed to be longer than in non-diapausing larvae. This suggests that initiation of larval diapause is reversible. The cages used for feeding the larvae were not appropriate diapausing sites and wandering larvae were not free to spin diapausing cocoons (although some diapausing larvae were found). Because larvae not finding an appropriate

diapausing substratum may have resumed feeding, it is possible that this study underestimated the proportion of larvae diapausing on each host. Moreover, only a subset of the small larvae were tested for diapause induction and the criteria used to score retrospectively all larvae as "diapausers" or "feeders" probably also resulted in conservative estimates of diapausing propensity.

A proportion of the "summer" larvae entered diapause and did not contribute to the second flight. The presence of such a diapausing strategy can be explained theoretically as a way of spreading the risk of reproductive failure in a temporally coarse-grained, unpredictable environment (Ward and Dixon, 1984, Lomnicki, 1988). A mixed diapausing strategy in which both tactics are expressed within the progeny of a single female has been found in the pitcher-plant mosquito (Istock, 1981) and in other insects (Tauber et al. 1986).

Phenotypic plasticity in host-specific diapausing propensity may be expected to evolve if the selective advantages of adopting a tactic (i.e. diapausing or not) reverse in successive summers and vary among hosts. Plant species may conceivably differ in their probabilities of being suitable between successive summers; for example, they may have an unequal chance of wilting in especially dry years. Although among-host differences in diapausing propensities have been reported in other insects (Tauber et

al. 1986, Horton et al. 1988), no host-dependent diapausing strategy was found in the OBL.

Interestingly, partial larval diapause in the summer was not observed in a previous study assessing development and mortality on different apple varieties (Onstad et al., 1986). In addition, diapause did not occur in larvae feeding on artificial diet at the photoperiod used in this experiment (Gangavalli and Aliniazee, 1985), although it was observed in my laboratory colony maintained under similar conditions. Such discrepancies between the diapausing strategy in my experimental populations and the populations studied in other work could be explained by geographic variation in maternal effects influencing diapause (Chapter 5), or by selection which reduced diapausing propensity in the laboratory colony of Gangavalli and Aliniazee (1985).

Relationship between pupal weight and fecundity in the field. Larval host did not affect female fecundity for any specific pupal weight, contrary to what has been found in other Lepidoptera species (Danthanarayana, 1975, Karowe, 1990). Using the relationship between pupal weight and fecundity established in the field, it was found that feeding on A increased mean fecundity by 26% over feeding on alternative hosts. Since females lay all their eggs in a few batches, their oviposition rate is probably not limited by the abundance of hosts (Courtney, 1984). This suggests that the field estimates of female lifetime fecundity are

accurate, even if they were derived using small oviposition cages in which oviposition sites are easy to find.

CONCLUSION

The results indicate that apple is a highly suitable host for the obliquebanded leafroller in the Okanagan valley. The high suitability of apple and its great abundance in the valley, are factors that would favor the evolution of an increased utilization of that crop by the obliquebanded leafroller. Comparisons of feeding performances of OBL populations exploiting habitats with variable host compositions are needed to determine whether the high feeding performance observed on apple in this study was the result of local response to selection for host use.

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Chapter 3:

LARVAL ACCEPTANCE OF HOST SPECIES WITHIN A POPULATION OF THE OBLIQUEBANDED LEAFROLLER

SUMMARY

The ballooning behavior of obliquebanded leafroller first instar larvae was studied in the laboratory. The objectives were to investigate the proximal factors influencing larval dispersal rates and to establish whether a correspondence exists between larval host acceptance and performance (as determined in Chapter 2). A dispersal bioassay was validated by demonstrating the presence of a positive correlation between larval host acceptance in the laboratory and in the field. Larval age and family origin, as well as host species attributes, were shown to influence larval dispersal rates. Seasonal changes in host plants changed slightly the rank order of larval host acceptance. Leaf texture and the availability of refugia on host plants seemed to be important factors influencing the rate of larval dispersal. Plant odor appeared to be used by the larvae to locate leaves. Nitrogen content of plant species corresponded to larval dispersal rates, but the cause of this association is unclear. Larval dispersal did not match host suitabilities as measured by larval performance. The relationship between host preference and suitability in the obliquebanded leafroller is discussed in an ecological and evolutionary perspective.

INTRODUCTION

An essential condition for evolutionary change in host-selection behavior is the presence of genetically-based variation in the behavioral rules that contribute to patterns of host use (Singer, 1986, Rausher, 1991, in press). Determining if such variation exists within insect populations is an important step toward evaluating whether a particular organism can respond genetically to changes in host availability or quality in its environment. Many characteristics of the insect and the plant can influence host-selection behaviors (Papaj and Rausher, 1983), and a knowledge of these factors is essential before estimating genetic variation in host responses.

Dispersal of first instar larva has been shown to be an important host-selection behavior in several Lepidoptera species (Lance, 1983, Barbosa et al., 1989). In the obliquebanded leafroller (OBL), *Choristoneura rosaceana*, air-borne larvae may contact many host species (Chapman and Lienk, 1971) that they can then accept or reject. The first objective of this study was to examine the proximal factors influencing larval dispersal in the OBL. The larval characteristics studied were 1) age, 2) genotype (family origin), and 3) feeding preference. The host plant characteristics investigated were 1) nutrient content, and 2) seasonal changes occurring in the hosts.

In Chapter 2, insects originating from an apple orchard were tested to estimate components of feeding

performance on apple and three alternative hosts throughout the summer. Insects from this same population were used to measure the rate of larval dispersal from the four host species, at the beginning and at the end of the summer. The second objective of this study was to determine whether the rank order of host acceptance corresponded to the rank order of host-feeding suitability in this population.

METHODS AND MATERIALS

Insect origin and rearing. Late instar larvae were collected at the end of May in 1988 from the apple orchard described in Chapter 2. The larvae were fed apple leaves until pupation and 110 arbitrarily selected mating pairs were used to initiate the colony.

From the first generation, a rearing procedure was adopted to minimize gene frequency changes in the colony. Females were individually caged with one male and access to water and allowed to oviposit on waxed paper. The egg masses from each female were kept in individual plastic cups. After hatching, seven larvae per female were raised individually on an artificial pinto bean diet (modified from Shorey and Hale, 1965) at 25 °C under a 16L:8D photoperiod. All experiments were carried out under these conditions unless otherwise stated.

In each generation, a maximum of two males and two females from each family were mated to perpetuate the colony (approximately 150 families were reared per generation).

Moths sharing common grandparents were not crossed. At the end of every generation, the number of families failing to contribute to the colony was recorded. All experiments were conducted using larvae from the seventh and eighth generations, except the measurement of larval dispersal on late summer hosts which was completed using second-generation larvae.

Origin of the host plants. The plants were collected from the sites described earlier (Chapter 2). The only modification to the plant collecting procedure was that branches were not divided in segments and that A and TA branches were collected from 24 marked trees located in the designated A block and TA patch.

The basic laboratory bioassay. The technique used to measure larval dispersal rates in the laboratory was similar to the method developed by Futuyma et al. (1984). Larvae originating from a female's first egg mass and less than 24 h old were transferred using a fine brush to the upper surface of the leaves of freshly collected host-plant branches. Each branch received one larva per leaf for a total of ten larvae, except apple branches which received two larvae per leaf. To prevent larval dispersal from one branch to the other, each branch was placed under a plastic container (diam 27.5 cm, height 30.5 cm) with two screened openings (22 x 14 cm) cut on opposite sides to permit air

circulation. The branch was kept in small water vials and prevented from touching the containers. Containers were placed in random order in front of two fans to provide a flow of air. Ninety min after transfer, the number of larvae remaining on each branch was counted.

Comparing laboratory and field dispersal rates. To ensure that variation in dispersal rates in the laboratory reflected variation in dispersal rates in the field, full-sib larvae were tested simultaneously in both environments. Fifty larvae per family were transferred to Red Delicious apple branches in the field. The branches were stripped of all except the first eight unfolded leaves and were prevented from touching other branches; five larvae were transferred to the first four unfolded leaves and five larvae to leaves five through eight. Transfers were conducted between 07:00 and 08:00 h on sunny days and the number and position of settled larvae was recorded eight to ten h later. One-hundred of the remaining larvae from each family were tested in the laboratory between 09:00 and 12:00 h on branches freshly collected from the same orchard where field dispersal tests were carried out. Twenty-two families of larvae were tested. The percentage of larvae remaining on apple within each family was arcsine transformed before estimating the correlation between laboratory and field dispersal rates.

Effect of plant species and seasonal change in leaf quality on dispersal rates. Phenotypic plasticity in dispersal rate was measured in the laboratory on four host species: Red Delicious apple (*Malus domestica*; A), trembling aspen (*Populus tremeloides*; TA), wild rose (*Rosa* sp.; R) and snowberry (*Shepherdia canadensis*; S). In each bioassay, larvae were transferred to two standard-size branches of each host, and two controls which consisted of plastic lids (15 cm diam) glued on sticks. In the fall tests (see below), fruits were removed from branches to standardize conditions between seasons.

Two series of bioassays were conducted to test the effect of presumed seasonal changes in plant quality. One series was done between August 15 and 30, 1988 (fall tests), and the second between June 28 and July 14, 1989 (summer tests). The data were analyzed using a two way ANOVA on the arcsine transformed percentages of larvae remaining on branches. Season and Host were considered as fixed effects.

Effect of leaf age, larval age and larval genotype, on larval dispersal. To investigate the effect of age on larval dispersal, full-sib larvae aged less than 2 h were tested on A branches in the laboratory. Other full-sibs from the same families were then tested 24 h later. A minimum of four replicates of eight larvae per full-sib group were transferred either to branches bearing only the first four unfolded leaves and the terminal unfolded leaves,

or to branches bearing only the fifth to eighth older leaves. Since A extension shoots produce new leaves about once every 10 days during the growing season, the distal leaves on a branch have "young" traits and leaves found further along the branch have "old" traits (Onstad et al., 1986, Schultz, 1983).

This experiment was conducted between June 16 and June 23, 1989, using 10 sib groups of larvae. The percentage of larvae remaining on each branch was arcsine transformed and data were analyzed using a 3-way ANOVA with sib groups considered as a random effect and larval and leaf age as fixed effects.

Feeding preference tests. To determine whether the rank order of larval dispersal rates corresponded to hatchling feeding preference, a "cafeteria test" in which pairs of host plants were offered to larvae was conducted. Aluminium dishes (3 cm diam X 1.5 cm high) were lined with moistened filter paper disks. A thin sheet of plastic perforated with four holes (0.8 cm diam.) around its circumference was placed on the surface of each filter paper (to facilitate larval movement). Four leaf disks (0.8 cm diam.), two for each host plant tested, were placed in the holes in alternating sequence, and a larva was transferred to the center of each plastic arena. Twenty larvae originating from at least three different families were used for each

replicate in which a pair of host plants was tested. Five replicates per plant combination were executed.

After a larva had been placed in the center of the arena, it was observed for a maximum of two min or until it contacted a leaf disk. The identity of the first plant contacted was noted. Then, the dishes were moved to a laboratory table and the position of the settled larva as well as leaf disk feeding damage was assessed after eight h. Experiments were conducted between June 24 and July 12, 1989.

Effect of host plant nitrogen and water content on larval dispersal. During the fall and summer tests, three samples of each plant species were collected every five days. Leaves were sampled between 09:00 and 10:00 h from marked trees and from designated R and S patches. The following quantities of leaves were collected every five days: 20 "young" and 20 "old" leaves from A (two leaves per tree in position three and seven for the "young" and "old" leaves, respectively), 24 composite leaves from R (two per bush), 28 opposing leaves from S (two per bush) and 20 from TA (two per tree). The leaves were immediately weighed to estimate their wet weight. They were then oven dried for 48 h at 60 °C, re-weighed to estimate their H_2O content, and macerated. Leaf N content was analyzed using an elemental analyzer (Carlo Erba TM, mod 1106). For each plant species and collection date, between three and five replicates were

tested for N content, and then pooled to yield a single estimate.

If larval dispersal rates are influenced by plant N or H_2O content, we would expect the rank order of larval dispersal rates, measured in both seasons from the four plant species, to be correlated with the rank order of the plants' N and H_2O contents. The estimates of N and H_2O content were pooled for each dispersal period. Plant species were then ranked across both seasons with respect to larval dispersal rates, N, and H_2O contents, using a one way ANOVA followed by Tukey tests. The degree of association between the series of ranked parameters was estimated by calculating Kendall's coefficient of rank correlation (Tau). The significance of the Taus was tested using a normal approximation (Sokal and Rohlf, 1981). One tailed P-values were used, since larvae are expected to prefer plant species with higher N and H_2O contents (Raupp and Denno, 1983). In all ANOVAs, type 3 sums of squares in the General Linear Model procedure of SAS were used (SAS Institute, 1985).

RESULTS

Comparison of laboratory and field dispersal rates. In the field, 34.5 ± 16.9 % (Mean ± s.d.) of the larvae settled on A leaves after 8 - 10 h. In the laboratory, 73.1 ± 8.8 % of the larvae remained on A branches after 1.5 h. In the field, most larvae settled along a principal vein on the

under surface of the leaves. They were found in small cavities made by feeding on the first layer of leaf cells. Other larvae were found either hiding in unfolded terminal leaves or having bored into the mid-vein. This observation demonstrates that larvae may explore the branch before settling and/or ballooning since no larvae were put directly on terminal unfolded leaves. There was a significant correlation between the percentage of larvae remaining on A branches in the laboratory and in the field ($r^2 = 0.44$, $P = 0.0007$, $n = 22$). Thus, variation in leaving rates among families in the laboratory reflects variation in leaving rates in the field.

Effect of plant species and seasonal change in leaf quality on dispersal rates. Larval leaving rates differed significantly among host plants ($F_{4,433} = 53.58$, $P < 0.0001$). In the fall tests, A was a preferred host, R and TA were ranked second and S and the control third (Table 3.1). More larvae stayed on R in the summer than in the fall, which resulted in the only change in rank order of dispersal between the summer and fall tests. Conversely, more larvae stayed on S in the fall than in the summer but it did not result in a change in rank order of dispersal between seasons (Table 3.1). Dispersal rates from A, TA and the control remained the same between seasons. The variation in host-specific dispersal rates between seasons

Table 3.1: Effects of plant species and phenology on the percentage of OBL larvae remaining on the host plant

Host [1]	% larvae remaining on the host		
	Fall [2,3]		Summer
A	68.8 a	NS	71.2 a
R	55.3 b	*	77.5 a
TA	51.6 b	NS	45.6 b
S	36.5 c	*	26.6 c
Control	30.3 c	NS	32.1 c

[1] A= apple, TA= trembling aspen, R= rose, S= snowberry.

[2] Means within the same column followed by the same letter are not significantly different, Tukey tests, $P < 0.05$.

[3] Means compared between seasons using T-tests: NS = $P > 0.05$, * = $P < 0.05$.

was detected in the ANOVA by a significant Season X Host interaction term ($F_{4,433} = 6.44$, $P < 0.0001$).

Effect of leaf age, larval age and larval genotype on larval dispersal. Twenty-four h old larvae were significantly more likely to stay on A leaves (Young leaves, 79.4 ± 16.2 % [Mean ± s.d.] ; old leaves 81.2 ± 11.2 %) than were larvae aged less than 2 h (Young leaves, 58.4 ± 20.0 %; old leaves, 60.2 ± 25.3, $F_{1,9} = 31.16$, $P = 0.0003$). Leaf age had no significant effect on larval dispersal rates ($F_{1,9} = 0.03$, $P = 0.8733$). Caterpillars originating from different families had significantly different dispersal rates ($F_{9,154} = 4.68$, $P = 0.0001$), suggesting that there was genetically-based variation within that population in ballooning rates from A. The effect of larval age on the propensity to leave A varied among families ($F_{9,154} = 2.00$, $P = 0.0432$).

In the field, 44.7 % of all settling larvae (n = 282) were found on "young" A leaves and 55.3 % on "old" leaves. These values are not significantly different from the values (50 %) expected under the assumption of equal preference between leaf classes (Interaction G-test, G = 1.60, NS).

Feeding preference tests. When the R x TA and R x S combinations were tested, a significantly greater proportion of larvae first contacted a R leaf disk (Table 3.2). However, R was not contacted first more often when offered with A. Since the leaf disk surface was just below the

level of the plastic arena, larvae probably did not use visual stimuli to locate a leaf disk, suggesting instead that hatchlings used olfaction to locate leaves. Therefore, rose odor may be particularly attractive to the larvae. An explanation for the similar probabilities of contacting A and R when offered in combination, may be that the combination of apple and rose odors blurred larval discrimination. The probabilities of contacting the hosts did not correspond to the rank order of host acceptance measured in the dispersal tests (compare Tables 3.1 and 3.2).

After contacting a leaf disk, a larva generally crawled under it and settled. However, some larvae moved on further, as indicated by the slight change in percentages between the type of leaf disk first contacted and the type chosen for settlement (Table 3.2). Inspection of the leaf disks revealed that in all cases, the larvae initiated feeding on a single disk. Larvae were always found under this disk at the end of the bioassay. For each host-plant combination, the probability of settling on each host type did not differ significantly from the probability of encountering first each host type (Table 3.2). Therefore, these results suggest that although host species differ in their capacity to attract larvae from a distance, no host discrimination occurs following contact on the basis of feeding preferences.

Table 3.2: Percentage of OBL larvae first contacting and then settling on leaf disks when offered a choice between host pairs

Host pair[1]	% of larvae first contacting the host[2]		% of larvae settling on the host
A	45.8		39.2
	ns	NS [3]	
R	54.2		60.8
TA	26.5		28.6
	*	NS	
R	73.5		71.4
S	30.6		35.5
	*	NS	
R	69.4		64.3
TA	49.4		47.2
	ns	NS	
A	50.6		52.8
S	53.2		57.5
	ns	NS	
A	46.8		42.5

1 A= apple, TA= trembling aspen, R= rose, S= snowberry.

2 Counts of larvae first contacting each host were compared to numbers expected under the null hypothesis that 50 % of the larvae should have contacted each host, using interaction G-tests: ns = $P > 0.05$, * = $P < 0.05$.

3 Counts of larvae settling on each host were compared to the number of larvae first contacting each host using interaction G-tests: NS = $P > 0.05$.

Effect of host-plant nitrogen and water content on larval dispersal. Mean N and H_2O contents were significantly different among plant species (Table 3.3). However, no statistically significant changes in N and H_2O contents were detected between seasons within a plant species.

The ranks in larval propensity to disperse from hosts were correlated with their ranks in N content (Tau = 0.886, P = 0.0011), but not with their ranks in H_2O content (Tau = -.043, P = 0.44; see Table 3.4 for ranked values used in the tests). "Young" and "old" A leaves differed in N and H_2O contents. However, no qualitative changes in the correlations between the ranks of larval dispersal and the ranks of N and H_2O content occurred when the parameters of the "young" A leaves were used instead of the parameters of the "old" A leaves.

DISCUSSION

The results of this study show that larval ballooning in the OBL is a complex process influenced by many factors intrinsic to the insects and to the plants. After encountering a host for the first time in the field, larvae either settled and initiated feeding or dispersed. There was a positive correlation between larval leaving rates from apple for sibs measured simultaneously in the laboratory and in the field. This suggests that it is adequate to use this

Table 3.3: Seasonal changes in leaf water and nitrogen contents in each of four host species

Host[1,2]	Period[3]	N (% ± s.d.)[4]	H_2O (% ± s.d.)[4]
A	S	2.52 ± 0.21 a	60.7 ±2.0 bc
A	F	2.57 ± 0.15 a	55.9 ± 0.5 c
R	S	2.56 ± 0.35 a	68.8 ± 2.1 a
R	F	2.35 ± 0.40 a	62.0 ± 6.4 abc
TA	S	2.27 ± 0.13 ab	58.3 ± 1.4 c
TA	F	2.27 ± 0.16 ab	56.6 ± 0.5 c
S	S	1.79 ± 0.21 b	60.7 ± 0.7 bc
S	F	1.98 ± 0.27 b	67.0 ± 1.1 ab

[1] A= apple, TA= trembling aspen, S= snowberry, R= rose.

[2] N and H_2O contents shown are for older A leaves.

[3] S = Summer, F = Fall.

[4] Means within columns followed by the same letter are not significantly different, Tukey tests, $P < 0.05$.

Table 3.4: Ranks given to plant species following Tukey tests: Smaller ranks correspond to low OBL dispersal rates from an host or to high nitrogen or water contents in a host

Host [1,2]	Period [3]	Larval dispersal [4]	Nitrogen	H_2O
A	S	1	1	2.5
A	F	1	1	3
R	S	1	1	1
R	F	2	1	2
TA	S	2.5	1.5	3
TA	F	2	1.5	3
S	S	3	2	2.5
S	F	3	2	1.5

1 A= apple, TA= trembling aspen, R= rose, S= snowberry.

2 Ranks calculated when "old" apple leaves parameters were included.

3 S = Summer, F = Fall.

4 Species assigned to more than one class in Tukey tests were given the average rank of the classes to which they belonged.

laboratory bioassay in assessing the proximal factors affecting larval ballooning.

Based on the feeding performances measured previously (Chapter 2), the rank order of larval host preference in the summer did not match the rank order of host-feeding suitability. The tendency of hatchlings to attempt dispersal from hosts was influenced by larval age and the familial origin of the larvae. Larval dispersal rates varied depending on host-plant species. The "cafeteria" tests demonstrated that larval feeding preferences did not modulate larval settlement choices. This suggests that larval assessment of plant nutrient and/or allelochemical contents is not the main determinant of host-specific ballooning rates in this species (see below). Host nitrogen contents were correlated with larval dispersal rates but further experiments are needed to confirm this relationship (see below). The rank order of larval dispersal from different hosts was not greatly affected by any seasonal transformations that occurred in the hosts.

Comparison of larval preference and performance. The host species influenced the hatchlings' propensity to disperse. The larvae, which originated from an apple orchard, were less likely to balloon from apple leaves than from other plant species in both seasons. When there is a high cost associated with host searching, as might be the case for ballooning larvae (Terry et al., 1989), the evolution of

high host specificity is more likely to occur when the most suitable hosts are easy to find (Otte and Joern, 1977, Wiklund, 1982). Given the above, the fact that apple was grown in a monoculture would have facilitated the evolution of a high acceptance for that host. In addition, optimal foraging models predict that hosts should be incorporated into the insects' diet in order of decreasing suitability (Jaenike, 1990). Feeding performance on the four hosts, a component of host suitability, was estimated for summer larvae (Chapter 2). The observed low dispersal rate from apple, a highly suitable host, is consistent with theoretical models. However, based on host-feeding performance, trembling aspen should probably have been ranked second and rose and snowberry third, which was not the case.

One explanation for this discrepancy could be that some of the assumptions in the optimal foraging and genetic models used earlier to predict host preference (see Introduction of Chapter 2 for a list of the models) do not apply in this system. These models assume that an optimal norm of reaction of host choice (the mean phenotypic response expressed by the members of a population in the presence of each host) will evolve in a panmictic population, independently of the probability of encounter with the potential hosts. However, if the relative acceptances of different hosts are genetically correlated, a change in acceptance of one host may result in changes in

the acceptance of alternative hosts. Therefore, sub-optimal choices of hosts may occur for certain rare hosts, or when the insect has the ability to exploit many hosts (Via and Lande, 1985). More specifically, because selection occurs more rapidly in a common than in a rare environment, models of the evolution of phenotypic plasticity predict that maladaptive phenotypes may be maintained for very long times in a rare environment (Via, 1987).

The population used to measure host larval responses was from an apple monoculture. This could have favored the evolution of a high apple acceptance, independently of the responses to other hosts (Chapter 6). Evidence for the presence of positive genetic correlations have been found between host-specific ballooning rates in the OBL (Chapter 6). If such a correlation was to exist between acceptance of apple and rose, this could lead to larvae having greater than expected staying rates on rose.

Alternatively, ecological factors other than feeding suitability of host may differentially influence larval fitness. These parameters should then be included in the estimates of host suitability to predict accurately host-specific dispersal rates. Leaf texture may be a factor determining host-specific ballooning rates in the OBL (see below). It could represent a constraint that would prevent larval settling on some hosts, irrespective of their suitability as food (Southwood, 1986). This would also

produce differences between the rank order of host preference and the measure of host suitability.

Seasonal changes in host-specific dispersal rates. Seasonal changes in hosts influenced larval dispersal. The effect of leaf age on the propensity of larvae to disperse from A was tested using young and old leaves from branches collected on the same date. The advantage of this procedure was that the effect of leaf age on larval dispersal could be assessed without using different populations of insects. Late instar larvae have been reported to prefer young leaves in the field (Chapman and Lienk, 1971, Carrière, pers. obs.). Accordingly, it was expected that hatchlings would show a preference for "young" leaves. No difference in dispersal rates of caterpillars from the leaf age classes was observed in the laboratory or in the field. This substantiates the results obtained in the fall and summer tests.

It is possible that changes in gene frequency that may have occurred in the colony between the fall and summer tests were responsible for seasonal changes in mean dispersal rates from S and R. Since host-specific dispersal rates have a strong genetic basis in this species (Chapter 6), this is a possibility that must be considered. However, careful rearing procedures were adopted to prevent changes in gene frequency in the colony. This was done by 1) keeping a high effective population size (> 200 breeding individuals per generation), 2) equalizing family

contributions to the next generation, and 3) preventing mating between individuals sharing grandparents. Moreover, most families raised in a given generation contributed to the next generation between the fall and summer tests (an average of two families per generation failed to contribute to the colony). No seasonal difference in dispersal rates from the control was observed, supporting the interpretation that no genetic changes in larval dispersal propensity occurred in the colony between the tests. Therefore, it seems that larvae reacted to seasonal changes in some hosts (R and S) but not in others (A or TA).

Host-plant quality, species, or phenology have been reported to affect ballooning in other Lepidoptera species (Schneider, 1980, Chapman et al., 1983, Ramachandran, 1987, Barbosa et al., 1989, Terry et al., 1989).

Effect of larval age and larval genotype on larval dispersal. Acceptance of apple as a settling site increased with larval age. Such change in host-selection behavior is a general phenomenon in herbivorous insects (Miller and Strickler, 1984, Singer, 1986).

A significant proportion of the variation in ballooning rates was also explained by the familial origin of the larvae. The larvae had been reared in common garden conditions for 6-7 generations prior to the tests, which suggests that maternal effects were not an important source of variation in ballooning. Variation in ballooning rates

could also result from within brood differences in larval size (Capinera and Barbosa, 1976, Lance, 1983). However, larval size did not differ among families within populations of the OBL (Chapter 6). Thus, the data indicate genetically-based variation in host-specific larval dispersal rates in the OBL. Genetically-based variation in larval propensity to leave hosts has been previously suggested to occur in other Lepidoptera larvae (Myers and Campbell, 1976, Futuyma et al., 1984, Berger, 1989).

Comparison of larval feeding preference and dispersal. Larval rank order of dispersal did not correspond to larval rank order of feeding preference. Thus, it seems that factors other than taste and/or olfaction modulate larval dispersal from hosts. When larvae were tested on A or R, which have relatively rough leaves compared to TA or S, they frequently settled under "free" leaves (i.e. leaves not touching any other leaves). When tested on TA or S, the larvae were recovered most of the time hiding between two touching leaves or between a leaf and a stem, but rarely under a "free" leaf. This suggests that leaf texture and refuge availability affect larval settlement on hosts. The importance of leaf texture is also supported by the observation that many more late instar larvae were found in the field on dwarf A trees bearing rough leaves than on dwarf trees with smoother and larger leaves, even when both

tree varieties were of similar size and located in the same field (Carrière, pers. obs.).

In the "cafeteria" tests, larvae always settled between the leaf disk and the moistened filter paper. This suggests that they had the same opportunity to hide when settling on all hosts and that finding a refuge did not affect larval choices. Therefore, the need to find a refuge may explain the different host-ranks obtained in the dispersal and feeding tests.

Effect of host plant nitrogen and water content on larval dispersal. Because of the potential role of leaf texture and refuge availability in influencing larval dispersal rates, the correlation between the rank order of ballooning from host plants and their rank order with respect to N content must be interpreted with caution. It is possible to rank hosts similarly when considering their N content, or their specific texture and availability of refuges. When considering host texture and refuge availability, R and A, which have a rough leaf texture compared to TA and S, would be given a rank of 1. Trembling aspen leaves often touched and overlapped in the dispersal tests, while S leaves rarely overlapped. Overlapping leaves may provide more refugia for larvae on TA than S; therefore TA would be ranked second and S third. Thus, the correlation between host plant N contents and larval dispersal rates may be spurious (see Table 3.4 for ranks of N content) and further tests

involving more plant species are necessary to corroborate this relationship.

CONCLUSIONS

Obliquebanded leafroller that were known to be in close association with an apple orchard for several generations showed a high feeding performance on, and a high preference for, apple compared to alternative hosts. Larval preference for apple remained constant throughout the season, and seasonal changes in host quality did not greatly influence larval host-selection behaviors. The presence of a significant "family" effect influencing larval acceptance of apple suggests that evolutionary changes in host responses could occur in the heterogeneous habitats exploited by this species.

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Chapter 4:

TRADEOFFS IN FEEDING PERFORMANCE ON DIFFERENT HOSTS WITHIN A POPULATION OF THE OBLIQUEBANDED LEAFROLLER.

SUMMARY

Evolutionary constraints on the ability of herbivores to achieve a high feeding efficiency on phytochemically similar hosts, while maintaining a high performance across phytochemically different hosts, is central in explaining the predominance of host specialization in phytophagous insects. Such feeding trade-offs are manifested within insect populations as negative genetic correlations in feeding performance on host-pairs. I tested the hypothesis that feeding trade-offs are present within a population of the obliquebanded leafroller. The feeding performance of specific families originating from an apple orchard was measured on four host-plant species in the laboratory. Within a host-pair, some families performed better on apple than on the other host, whereas other families performed equally well on apple and the other host. This indicates that genetic variation in feeding specialization is present in the population. Feeding trade-offs were detected after correcting for the potential impact of general vigor and/or maternal effects. Significant "family" effects were found in all traits (i.e. live weight, diapausing propensity, development time, pupal weight, egg-to-pupa growth rate), suggesting that they would respond to selection. Evidence

for the presence of a negative genetic correlation between within family propensity to diapause and live weight, and of a positive correlation between propensity to diapause and development time was found. In addition, a negative genetic correlation between live weight and development time and a positive correlation between live weight and pupal weight were apparent. Such genetic relationships could constrain the evolution of fast development time if a high propensity to diapause is adaptive in the summer.

INTRODUCTION

Host chemistry is a major constraint affecting the evolution of insect-plant associations (Jaenike, 1990). Numerous models on the evolution of diet breadth in phytophagous insects recognize this by assuming that a high physiological performance in feeding on phytochemically similar hosts is achieved at the expense of a low performance on phytochemically different hosts (Futuyma and Philippi, 1987). This notion stems from the premise that for an equal detoxification performance on similar hosts, specialized enzymatic systems are less costly to maintain than generalized systems (Levins, 1968). Consequently, specialist insects are expected to be more efficient and to grow faster or larger than generalists, when using the host plant of the specialist. The cost of evolving this high feeding efficiency for the specialist is that it will be relatively ineffective in using different hosts.

If present, feeding trade-offs will slow the joint evolution of high feeding performance across the potential hosts of an insect (Via and Lande, 1985, Via, 1987). Consequently, trade-offs would favor specialization in host-selection behavior, if the evolution of avoidance of a poor host, or preference for a good host, occurs at a faster rate than the evolution of high feeding performance across hosts (see Gould, 1984, 1988 for single locus model).

The advantages associated with polyphagy (e.g. increased life-time fecundity) may often surpass the

disadvantages of using hosts on which the insect is not well adapted (Wiklund, 1982, Rossiter, 1987, Bernays and Graham, 1988). Therefore, the impact of feeding trade-offs on host-range evolution may be more important in populations or species in which search costs are low, and specialization may only be favored in particular environments. Nevertheless, physiological constraints imposed on insect feeding efficiency could act as a central factor favoring specialization and partly explain why the majority of phytophagous insect species have a specialized diet (Strong et al., 1984, Jermy, 1984, Jaenike, 1990).

Three types of comparative experiments have been used to assess whether feeding trade-offs are widespread in herbivorous insects. The first compares the feeding performance of generalist and specialist species on the hosts of the specialist. However, selective factors other than the discrepancy in feeding efficiency between the specialists and generalists can affect the life-history traits used for comparisons, rendering the results of these experiments difficult to interpret (Rausher, 1984). The second type of experiment compares individuals of the same species sampled from distinct populations associated with different hosts (Via, 1990). These experiments reveal whether genetic differentiation in feeding performance has occurred. However, they do not separate the potential effects of genetic drift, differential selection and genetically-based feeding trade-offs in generating the

divergences in feeding performance among the populations (Strong et al., 1984, Futuyma and Philippi, 1987, Gould, 1988, Jaenike, 1990). The last method consists of measuring the genetic covariation in feeding performance on different hosts among genotypes originating from the same population of insects. In these comparisons, the presence of negative genetic correlations in feeding performance traits on host-pairs indicate that feeding trade-offs are potentially important influences on the evolution of host-selection behaviors in phytophagous insects (Rausher, 1984, Via, 1984 a, b).

The search for negative genetic correlations in feeding performance across hosts has stimulated many studies, but such correlations have not been detected during most investigations to date (reviewed in Futuyma and Peterson, 1985, Futuyma and Moreno, 1988, Via, 1990). As a result, feeding trade-offs have been dismissed as an important factor favoring specialization in phytophagous insects (Bernays and Graham, 1988; but see Rausher, 1988). The value of a genetic correlation between two traits is determined by the overall effects of all genes segregating for both characters (Falconer, 1981). Thus, for genetic correlations in feeding performance traits to be good approximations of the magnitude of feeding trade-offs, it must be assumed that the genetic covariance measured across hosts is mainly due to pleiotropic or linkage disequilibrium

effects influencing the traits via their consequence for detoxification performance.

The overall genetic correlations in life-history traits that are measured on different hosts may be misleading, however, if animals are not tested in environments in which they have evolved (Moller et al., 1989). It is known that the values of genetic correlations between life-history traits are likely to become more positive in novel environments (Service and Rose, 1985, Bell and Koufopanou, 1986, Scheiner et al., 1989, Holloway et al., 1990). This variation in the value of the genetic correlations would arise if a change occurred in the number and/or effects of the genes contributing to the traits in each environment (Falconer, 1981, Via, 1984 b). To date, most experiments measuring the magnitude of feeding trade-offs have been conducted in the laboratory. Therefore, positively biased estimates of the genetic correlations may have arizen if some of the measured genotypes were pre-adapted to the laboratory conditions, a phenomenon that was recognized by Jaenike (1990) as the general vigor effect. This implies that the lack of an overall negative genetic correlation in feeding performance on different hosts does not necessarily mean that feeding trade-offs do not exist, but rather that they were not the dominant factor that affected the patterns of genetic correlations in feeding performance. It is thus possible that genetic correlations, adjusted for potential general vigor effects in laboratory experiments, would

reflect more adequately the magnitude of feeding trade-offs in herbivorous insects (Futuyma and Philippi, 1987, Jaenike, 1990).

In this chapter, I report the results of a laboratory experiment that was conducted to determine whether genetically-based feeding trade-offs are present in the obliquebanded leafroller (OBL). The insects were fed on four host species in the laboratory. A statistical method was developed to separate the potential effect of general vigor from the effect of feeding trade-offs in influencing the overall value of the genetic correlations.

MATERIALS AND METHODS

Obliquebanded leafrollers were collected from an apple orchard. The source population had been present in the orchard for at least 10 generations (Chapter 2). This association with apple may have favored the evolution of "specialized" enzymatic systems and increased the probability of detecting feeding trade-offs when the insects are fed on hosts originating from different plant families.

Definitions of specialist and generalist. Within a population, specific genotypes may perform better on one host than on another host, whereas other genotypes may perform equally well on both hosts. In this chapter, such genotypes will be designated as specialists and generalists, respectively .

Other authors have characterized genotypes within a population on the basis of the mechanism of expression of the genes segregating for the feeding performance traits on different hosts (Futuyma and Philippi, 1987, Via, 1984b, 1987). Within a population, the genotypes were designated as generalists when a set of genes influence a feeding performance trait in similar ways on different hosts. On the other hand, if a set of genes has opposite effects on a feeding performance trait on different hosts, or if the trait is influenced by different genes on diverse hosts, the genotypes were designated as specialists. Whenever used, this later definition will be explicitly designated.

Experimental design and feeding procedure. A full-sib experimental design was used to measure the feeding performance of different genotypes (families) on apple and three alternative hosts. The "family" effects and genetic correlations in feeding-performance traits thus result from potential additive, non-additive and maternal effects (Falconer, 1981, Via, 1984b).

The methods of collection of the insects and plants, and the procedures adopted to measure the fitness components and feed the insects are described in detail in Chapter 2. Briefly, 160 insects from each of 11 families were divided equally into four groups and fed on four host plant species: Red Delicious apple (*Malus domestica*; A), trembling aspen (*Populus tremeloides*; TA), wild rose (*Rosa* sp.; R) and

snowberry (*Shepherdia canadensis*; S). For each Family x host combination, four hatchlings aged less than 24 h were transferred to each of 10 cages. The 10 cages were distributed randomly as a group in a section of the growth chamber in which a temperature of 25 °C and a 16L:8D photoperiod were maintained. Every day, each group was re-located randomly to minimize micro-climatic effects on larval growth. The plants used to feed the insects were kept in plastic vials filled with water and changed every three days. When plant material was replaced, the pupae found in the feeding cages were weighed and total development time was recorded in multiples of three days.

The fitness components analyzed here are larval live weight at 18 days (LW; an index of growth rate), the proportion of surviving larvae that initiated diapause instead of continuing development after 18 days (DIAP), total development time (DT), pupal weight (PW) and egg-to-pupa growth rate (GR), which was obtained by dividing individual pupal weight by their estimated total development time. Diapausing propensity within a family is considered a fitness component under the assumption that the genetic contribution of individuals to future generations is correlated to phenotypic variation in that trait (see Discussion).

Comparison of laboratory and field adult size. To estimate the effect of the rearing conditions on insect growth, the

size of moths captured using pheromone traps near the site where the plants were collected was compared to the size of insects obtained from the feeding experiment. The field moths used in the comparison were captured during the same period the laboratory moths emerged. Male forewing length, measured as the distance between the extremity of the tegula and the forewing tip was used as an index of size (Miller, 1976). The validity of this index as a general indicator of size was verified by regressing pupal weight on forewing length in laboratory produced males. The difference between moths mean size was tested using a Satterthwaite's approximate t statistic and the homogeneity of variances was tested using the folded form of the F statistic (TTEST procedure, SAS, 1988).

Experimental analysis

Live weight and diapausing propensity. The larvae from the 11 families hatched within a two week period. To investigate whether larval weight was influenced by the date of onset of feeding, variation in LW was analyzed using an ANOVA in which the families initiating feeding on the same day were nested within date (Host, Sex, Family [Date] and Date were the four effects considered). Two families were excluded from the analysis because they were transferred to the four hosts species individually on a given date. To estimate the date effect on the incidence of larval diapause, the proportion of diapausing larvae within the

same nine families were analyzed using a two-way ANOVA, in which the effect of Host and Date were investigated.

The significance of between-family effects on DIAP and LW were analyzed using a three-way log-linear model (LLM) and a three-way ANOVA respectively. A LLM was used to analyse DIAP since they are proportional data. The genetic correlations between diapausing propensities on different hosts were estimated by computing correlations of family means (Rausher, 1984, Via, 1984b). A principal component analysis was conducted to explore the factors that influenced the patterns of diapausing propensities observed for the families across the four hosts.

The genetic correlation between two traits expressed on a host is of interest to determine whether these characters can evolve independently (Via, 1984 b). Instead of estimating the genetic correlations between traits expressed on each host, the relationship between the relative value of pairs of characters expressed by the genotypes on all hosts were estimated. Calculating an across-host correlation instead of the relationships expressed on each host increased the sample size and therefore the power of detection of such relationships. To calculate the across-host relationships, the performance of each genotype on the four hosts were transformed to a unit normal distribution ($x'_i = [x_i - X]/S_X$, where x_i is the mean value of the i-th family, X is the mean across all families on a host, and S_X is the standard deviation among family means observed on the

same host). Such a transformation standardizes the mean value of a character observed for a family on a given host by eliminating scale effects (Wade, 1990). Thus, the relative performances of the families observed on the four hosts become comparable. These performance measures were pooled to estimate an overall relationship between pairs of traits in the 11 families. The correlations between the relative DIAP, LW, and the relative fitness components (DT, PW, and GR) were computed separately for each sex. Mean character values calculated from less than three observations were not retained to increase the precision of the estimates.

Adult fitness components. The contribution of the different factors on the phenotypic variation in DT was analyzed using a four-way LLM. A LLM was used because development time was recorded in multiples of three days. The significance of the between-family effects on PW and GR was estimated using three-way ANOVA's.

Instead of computing the standard product-moment correlations of family means in PW and GR on the host-pairs, the genetic correlations were approximated using the least-squares means (LSM), estimated by the GLM computing procedure (SAS, 1988) for every combination of Family X host. The LSM are the population means for the combinations of Family X host that would be expected for a balanced design (Searle et al., 1980). Their values are estimates of

the feeding performances of each family on each of the four hosts and do not include effects that are not directly related to feeding efficiency.

There are three advantages of using LSM instead of family means in computing genetic correlations. First, LSM are estimated for each effect of interest by keeping all other covariates at their average values (Searle et al., 1980). This procedure excludes any undesired effect from the correlations.

Second, the differences between the LSM estimated for each family on host-pairs can be tested statistically. The significance of the differences between the LSM estimates of PW and GR for each family on the host-pairs A-R, A-S and A-TA were tested. These tests allow one to visualize directly the genetic variation in specialization on A that was present within this population, given that for each host-pair, genotypes that performed better on A were separated from genotypes that performed equally well on the two hosts. A Bonferonni procedure was used to maintain an experimentwise error rate of 0.05 in the comparisons of the feeding performances of each genotype on the host-pairs. One-tailed statistical tests were applied since the genotypes were assumed to already have evolved a high feeding performance on A.

The third advantage of the LSM procedure is that general vigor (or maternal effects) can be corrected from the approximations of the genetic correlations, by

subtracting from the LSM estimated for each combination of Family x host, the LSM calculated for the corresponding family. Whereas the LSM for every combination of Family x host estimates the feeding performance of a given family on that host, the LSM estimated for a family is the arithmetic average of the mean feeding performance of the family on each host (Searle et al., 1980). Therefore, the operation ($LSM_{Family\ X\ host} - LSM_{Family}$) corrects for the general vigor of a given genotype, or for a maternal effect that would introduce non-genetic variation among the average feeding performance of the genotypes on the four hosts. This latter operation is somewhat equivalent to the correction that was executed by Futuyma and Philippi (1987).

The LLM's were computed using the program BMDP4F (BMDP Institute, 1990). The principal component analysis was performed using the PRINCOMP procedure (SAS, 1988). All ANOVA's were performed in the GLM procedure using type 3 sums of squares and the TEST option in the RANDOM statement, which means that significance tests were estimated using Satterthwaite approximations (SAS, 1988). Effects including the Family factor were considered random, whereas the other effects were considered fixed.

RESULTS

Comparison of laboratory and field adult size. Wing length was significantly correlated with pupal weight in males ($r^2 = 0.80$, $n = 128$, $P = 0.0001$), showing that it is a good

index of size in the OBL. Field and laboratory males had similar mean wing lengths (0.88 ± 0.07 cm [Mean ± SE] vs 0.89 ± 0.05 cm respectively; t = -0.9538, P = 0.3418). The variance in wing length in field moths was greater than in laboratory individuals (F' = 1.72, df = 83, 127, P = 0.006). This suggests that environmentally induced variance in feeding performance was reduced by the controlled conditions of the laboratory.

Live weight and diapausing propensity. Groups of families that had initiated feeding on different dates had similar larval growth or diapausing propensities on the four host species. The date of onset of feeding did not affect the average larval weight on the four hosts (Date effect, F = 1.64, df = 2, 289, P = 0.1967 ; ANOVA computed on ln transformed LW) or the difference in mean larval weight of the family groups between hosts (Date x host effect, F = 1.63, df = 6, 17, P = 0.2001. Similarly, the date of onset of feeding had no influence on the average diapausing propensity of the family groups on the four hosts (Date effect, F = 0.34, df = 2, 23, P = 0.7122; ANOVA computed on arcsine transformed DIAP), nor on the difference in the diapausing response of the family groups on the hosts (Host X date effect, F = 0.36, df = 6 , 23, P = 0.8943).

Live weight and the propensity to diapause on the four host species are reported for the 11 families in Tables 4.1 and 4.2. The familial origin of the larvae significantly

Table 4.1: Mean larval weight (ln live weight in mg) of 11 families of the OBL. Mean weight (X), standard error (SE) and sample size (N) are given. Hosts are apple (A), rose (R), snowberry (S) and trembling aspen (TA).

			FAMILY										
HOST	SEX		1	2	3	4	5	6	7	8	9	10	11
A	M	X	2.99	3.12	2.84	3.29	3.22	3.07	2.34	1.55	2.59	3.91	2.14
		SE	0.45	0.46	1.61	0.11	0.17	0.41	0.89	.	0.34	0.52	0.72
		N	6	4	2	5	16	4	2	1	4	4	3
	F	X	3.67	3.62	4.75	3.58	4.00	4.37	1.15	4.10	2.71	4.20	2.79
		SE	0.41	0.53	.	0.21	0.27	0.29	.	0.13	.	0.32	0.53
		N	6	2	1	9	3	2	1	5	1	4	6
R	M	X	4.03	4.08	3.10	3.37	3.47	3.86	4.27	2.23	2.02	4.19	3.58
		SE	0.25	0.12	0.68	0.22	0.16	0.28	0.25	0.60	0.65	0.11	0.42
		N	8	11	4	2	15	5	3	3	3	7	2
	F	X	4.60	4.31	4.33	3.82	3.75	4.53	3.02	4.31	3.50	4.65	4.01
		SE	0.16	0.12	.	0.07	0.19	0.25	1.93	.	.	0.16	0.33
		N	3	11	1	10	6	5	2	1	1	7	3
S	M	X	3.87	3.70	2.92	2.97	3.00	3.78	3.04	3.09	3.36	4.37	3.29
		SE	0.21	0.21	0.36	0.17	0.21	0.33	0.84	0.38	0.22	0.06	0.49
		N	10	7	2	8	7	3	4	4	3	6	4
	F	X	3.47	3.94	2.82	3.43	3.16	3.94	3.97	3.68	2.80	4.31	3.42
		SE	0.56	0.17	0.30	0.16	0.38	0.25	0.41	0.31	.	0.12	0.17
		N	6	9	5	6	6	7	3	3	1	12	8
TA	M	X	3.50	3.34	1.91	2.46	2.68	2.98	2.45	1.56	.	3.26	2.12
		SE	0.22	0.18	0.41	0.18	0.37	0.78	0.30	0.29	.	0.36	0.16
		N	7	8	4	6	6	2	6	3	0	3	5
	F	X	3.40	3.07	2.77	2.64	3.41	3.06	2.50	2.13	.	3.41	2.22
		SE	0.25	0.23	0.25	0.14	0.17	0.22	0.96	0.87	.	0.32	0.39
		N	9	8	5	10	9	3	2	2	0	8	3

Table 4.2: Proportion of the surviving larvae that had initiated diapause after 18 days of feeding in 11 families of the OBL. Hosts are apple (A), rose (R), snowberry (S) and trembling aspen (TA).

	FAMILY										
HOST	1	2	3	4	5	6	7	8	9	10	11
A	0.12	0.33	0.50	0	0	0.22	0.25	0.27	0.40	0.11	0.33
R	0	0	0.37	0.12	0.04	0	0.45	0.61	0.56	0	0.29
S	0.06	0	0.30	0.12	0.12	0.07	0.36	0.23	0.25	0	0
TA	0.05	0.15	0.44	0.20	0	0.14	0.36	0.12	0.67	0.07	0.44

influenced the propensity to diapause on the four hosts, suggesting that the variation in the propensity to diapause was genetically based in this population (see Table 4.3; Diapause X family effect). The saturated LLM describing the larval diapause data did not fit well (Table 4.3; Host X diapause X family effect). This indicates that the differences among the diapausing responses of the families on one host were not maintained across all hosts, and implies that trade-offs in diapausing propensity on different hosts could be present. The program BMDP4F (BMDP Institute, 1990) was used to investigate the nature of the significance of the third order effect. To do this, the cells that were the most likely to be responsible for the lack of fit of the model were located (by finding the cells with the largest Freeman-Tukey deviates). The significance of the contribution of each of these cells to the model was then estimated after they had been deleted in a stepwise manner. This procedure showed that the lack of fit of the saturated model was due to four cells; families 2 and 7 had a relatively large number of larvae feeding on host A and TA, respectively, whereas families 8 and 11 had a relatively large number of larvae diapausing on hosts R and TA, respectively. Thus, the inconsistency in the patterns of diapausing response of the 11 families on the four hosts is due to the responses of four families.

The genetic correlations in diapausing propensity were all positive (Table 4.4); a genotype that had a high

Table 4.3: Analysis of diapausing propensity on four different host species in the OBL using a log-linear model

SOURCE	d.f.	G	P
Host X family	30	37.43	0.165
Host X diapause	3	6.55	0.087
Diapause X family	10	99.10	< 0.001
Host X diapause X family	30	49.85	0.013

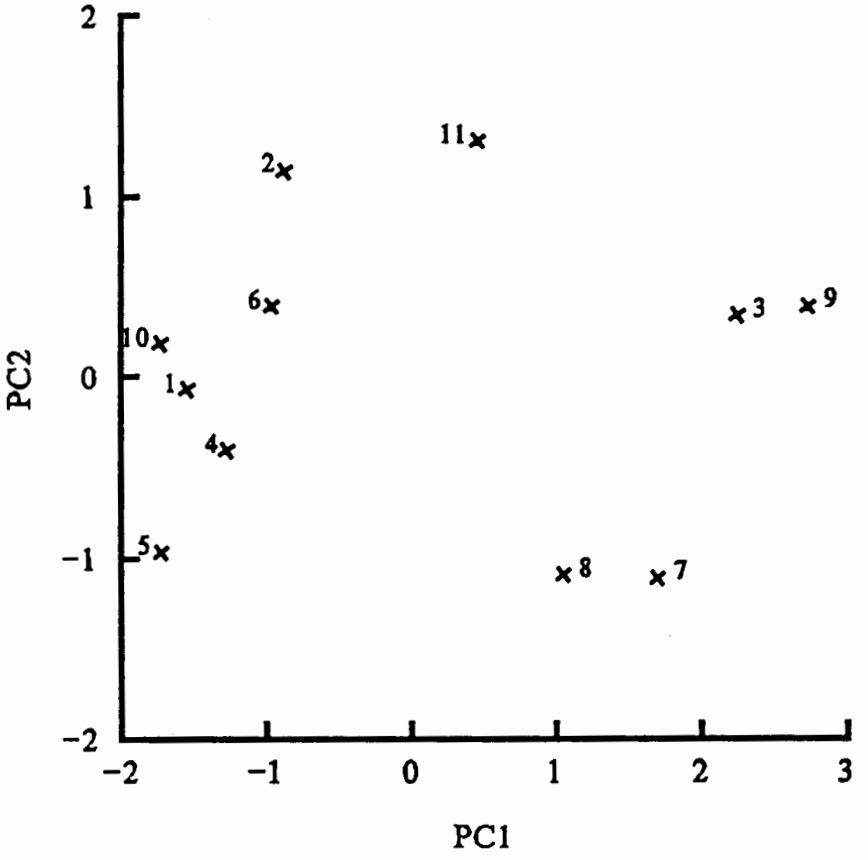
Table 4.4: Estimates of genetic correlations of larval diapausing propensity on host-pairs for OBL larvae fed on four different host species

	Apple	Rose	Snowberry	Trembling aspen
Apple	--	0.564	0.437	0.728 ** [1]
Rose		--	0.780 ***	0.677 *
Snowberry			--	0.503
Trembling aspen				--

[1] * P = 0.02, ** P < 0.01, *** P < 0.005.

diapausing propensity on one host tended to have similar responses toward all hosts. The first and second components of the principal component analysis summarizing thediapausing responses of the 11 families across the hosts accounted for 71.1 % and 17.4 % of the total variance, respectively. The correlations between the first component and the diapausing propensities were 0.48 (on A), 0.53 (on R), 0.48 (on S) and 0.51 on (TA), whereas they were 0.58 (on A), -0.33 (on R), -0.63 (on S) and 0.39 (on TA) between the diapausing propensities and the second component. Thus, the first component measures the overall diapausing incidences of the families on all tested hosts and the second component contrasts their diapausing propensities on bushes versus trees. The distribution of the families with respect to the first component suggests that the sampled insects were divided in two groups (Figure 4.1); families with a high diapausing propensity (3, 7, 8 and 9) and families with a low incidence of diapause (1, 2, 4, 5, 6, 10). This finding is consistent with the presence of positive genetic correlations in diapausing propensities previously found on host-pairs. The distribution of families with respect to the second component also provides information on the nature of the "interaction" in the across host diapausing responses of the four families that had been detected previously (Figure 4.1). Families 7 and 8 had high diapausing propensities on bushes compared to their diapausing response on trees, and families 2 and 11 had an inverse response,

Figure 4.1. Principal components of the diapausing responses of the 11 families across the hosts. The first component measures the overall diapausing propensities of the families on the four hosts. The second component contrasts their diapausing response on bushes (R and S) versus trees (A and TA). The crosses indicate the values of the components corresponding to each family.


2
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suggesting a trade-off in the expression of diapause on bushes versus trees was present in this population.

Among-family and among-host variation in LW was detected (Table 4.5), but no significant Family x host interaction was present. This suggests a significant heritability of live weight and consistant differences in live weight across the four hosts among the genotypes. Females were larger than males after 18 days and larval weights on different hosts were significantly different in both sexes (Table 4.5 and 4.6), showing that the plants were nutritionally different to the larvae.

There was a negative correlation between the families' relative diapausing propensities and their relative mean larval weight attained on a host. The value of the correlation coefficients were -0.541 ($P = 0.0007$, $n = 36$) and -0.443 ($P = 0.011$, $n = 32$) for males and females, respectively. Thus, families that had a relatively slow larval growth rates on a host tended to have a relatively high incidence of diapause on the same host. Furthermore, the relative propensity to diapause on a host was correlated with relative development time and egg-to-pupa growth rate in males and with development time in females (Table 4.7). The relative live weights were also correlated with the relative values of all the adult fitness components measured in males and females. A significant genetic correlation between characters suggests that common genes influence the expression of the characters (Falconer, 1981, Via, 1984b).

Table 4.5: Analysis of variance of larval weight (ln live weight in mg) after 18 days of feeding in the OBL

SOURCE[1]	MS	d.f.	DENOMINATOR MS	F	P
Family	5.169	10; 13.48	1.327	3.895	0.011
Host	16.169	3; 39.35	0.771	21.257	0.0001
Sex	11.719	1; 13.05	0.906	12.937	0.0032
Family X host	0.840	29; 29	0.499	1.684	0.083
Family X sex	1.017	10; 35.18	0.500	2.032	0.059
Host X sex	1.351	3; 47.19	0.502	2.690	0.057
Family X host X sex	0.499	29; 351	0.514	0.971	0.512

1 $r^2 = 0.51$

Table 4.6: Mean larval weight (± SE; ln live weight in mg) attained on apple (A), rose (R), snowberry (S) and trembling aspen (TA) in both sexes of the OBL.

SEX	HOST[1]			
	A	R	S	TA
M	3.04 ± 0.13 ab	3.65 ± 0.11 a	3.46 ± 0.11 a	2.71 ± 0.12 b
F	3.62 ± 0.15 b	4.15 ± 0.10 a	3.67 ± 0.10 b	3.03 ± 0.10 c

[1] Means followed by the same letter within a line are not significantly different (one-way ANOVA followed by Tukey tests, $P < 0.05$).

Table 4.7: Genetic correlations between unit-normal transformed diapausing propensity (DIAP), larval weight after 18 days of feeding (LW) and development time (DT), pupal weight (PW) and egg-to-pupa growth rate (GR) for males and females in the OBL.

SEX		DT	PW	GR
M	DIAP	0.642^{***} [1] (n=34)	- 0.120 (n=34)	-0.402^{*} (n=34)
	LW	-0.816^{***} (n=33)	0.572^{***} (n=33)	0.827^{***} (n=33)
F	DIAP	0.465^{**} (n=30)	0.114 (n=30)	- 0.227 (n=30)
	LW	-0.669^{***} (n=30)	0.506^{**} (n=30)	0.738^{***} (n=30)

[1] * P = 0.017, ** P < 0.01, *** P < 0.001

Thus, genes segregating for larval growth apparently had an impact on the variation in adult weight and development time. However, genes segregating for larval diapause, although influencing larval growth, only affected one adult fitness component (development time).

Adult fitness components. Family means of adult fitness components measured on the four hosts are reported in Table 4.8 for males and females. Sex, host and family influenced the distribution of development times (Table 4.9). More specifically, males generally developed more rapidly than females, females had relatively slow development times on TA (Chapter 2), and heritable differences in development time appeared to be present in this population. The significance of the third order effect shows that the pattern of variation in the among-family distribution of development times was not maintained across the four hosts and indicates that trade-offs in development times on different hosts could be present. Separate two-way LLM conducted for each sex on each host demonstrated that the Family effect was significant in all cases ($P < 0.01$), except for males on A.

Significant among-family variation was found for PW and GR but the Family x host interaction was only significant for GR (Table 4.10). F tests involving the Host and Sex effects were not valid when using Satterthwaite approximations because more than one fixed effect had to be combined in the numerator to meet the mean square

Table 4.8: Mean pupal weight (PW; in mg), development time (in days) and egg-to-pupa growth rate (GR; in mg/day) by sex and family in the OBL. Standard errors are in parentheses. Hosts are apple (A), rose (R), snowberry (S) and trembling aspen (TA).

			FAMILY										
HOST	SEX	TRAITS	1	2	3	4	5	6	7	8	9	10	11
A	M	WT	55.0	52.2	50.7	50.8	49.1	54.0	53.5	50.0	38.5	57.5	56.0
			(2.9)	(3.5)	(4.8)	(1.9)	(2.0)	(5.3)	(6.5)	(-)	(6.6)	(4.2)	(-)
		DT	26.5	27.0	31.0	25.2	26.8	30.2	31.5	36.0	30.5	23.2	24.0
			(1.8)	(1.2)	(5.0)	(.7)	(.8)	(3.8)	(4.5)	(-)	(4.1)	(2.2)	(-)
		GR	2.12	1.96	1.80	2.02	1.87	1.98	1.76	1.39	1.41	2.58	2.33
			(.17)	(.21)	(.53)	(.10)	(.12)	(.39)	(.46)	(-)	(.37)	(.36)	(-)
	F	WT	91.6	77.0	95.5	93.0	79.2	101.0	113.0	98.8	83.0	99.7	84.2
			(5.4)	(3.0)	(10.5)	(2.3)	(16.1)	(23.0)	(-)	(3.3)	(-)	(7.5)	(6.2)
		DT	26.4	28.5	28.5	28.9	32.2	27.0	36.0	28.8	33.0	24.7	31.8
			(1.1)	(1.5)	(4.5)	0(.8)	(2.6)	(3.0)	(-)	(.7)	(-)	(.7)	(2.4)
		GR	3.49	2.70	3.47	3.23	2.61	2.69	3.14	3.25	2.51	4.05	2.75
			(.25)	(.04)	(.92)	(.08)	(.68)	(.44)	(-)	(.09)	(-)	(.37)	(.32)
R	M	WT	47.7	46.0	43.5	39.5	40.6	43.2	52.3	39.0	47.7	45.5	56.0
			(1.1)	(2.1)	(2.2)	(2.5)	(2.4)	(4.8)	(.7)	(3.0)	(4.7)	(1.6)	(5.0)
		DT	24.0	24.0	27.0	25.5	28.1	28.4	25.0	34.0	32.0	21.7	25.5
			(1.2)	(.9)	(2.1)	(1.5)	(1.0)	(3.8)	(4.0)	(4.4)	(2.6)	(.7)	(1.5)
		GR	2.02	1.94	1.62	1.55	1.49	1.68	2.20	1.20	1.53	2.11	2.21
			(.11)	(.15)	(.09)	(.01)	(.13)	(.31)	(.33)	(.24)	(.26)	(.11)	(.33)
	F	WT	72.5	68.9	73.0	71.6	65.1	75.0	82.5	67.0	50.0	82.8	80.3
			(1.5)	(2.9)	(-)	(2.2)	(7.8)	(3.9)	(7.5)	(-)	(-)	(3.3)	(1.8)

Table 4.8 cont'd

		DT	25.5	26.5	27.0	29.1	34.2	27.6	27.0	27.0	36.0	25.0	28.0
			(1.5)	(.6)	(-)	(.6)	(1.9)	(2.9)	(3.0)	(-)	(-)	(1.3)	(1.0)
		GR	2.85	2.63	2.70	2.48	1.99	2.86	3.06	2.48	1.39	3.35	2.88
			(.11)	(.14)	(-)	(.11)	(.33)	(.34)	(.06)	(-)	(-)	(.19)	(.14)
S	M	WT	45.2	41.4	44.0	44.7	41.6	45.7	50.0	33.7	40.3	52.0	44.5
			(2.0)	(1.0)	(3.0)	(2.5)	(6.1)	(4.1)	(3.5)	(3.1)	(2.3)	(3.1)	(4.9)
		DT	23.0	24.0	27.0	30.4	28.2	28.0	26.0	30.7	28.0	22.5	26.2
			(1.0)	(.9)	(3.0)	(1.4)	(2.0)	(2.6)	(3.6)	(2.8)	(1.0)	(.9)	(1.4)
		GR	1.99	1.74	1.63	1.51	1.54	1.67	2.02	1.14	1.45	2.33	1.73
			(.16)	(.07)	(.07)	(.13)	(.28)	(.25)	(.37)	(.17)	(.13)	(.21)	(.27)
	F	WT	74.8	63.8	68.4	65.1	57.7	69.1	87.4	66.7	90.0	76.7	73.7
			(4.8)	(3.7)	(3.2)	(2.1)	(7.0)	(1.4)	(5.3)	(2.9)	(-)	(3.3)	(3.6)
		DT	28.3	26.7	31.2	32.1	34.0	27.4	33.6	32.0	36.0	25.3	29.6
			(2.1)	(.8)	(1.5)	(.8)	(2.9)	(1.4)	(2.4)	(2.0)	(-)	(.5)	(1.1)
		GR	2.71	2.42	2.21	2.04	1.86	2.56	2.67	2.11	2.50	3.05	2.49
			(.2)	(.18)	(.13)	(.09)	(.4)	(.14)	(.28)	(.2)	(-)	(.18)	(.07)
TA	M	WT	52.4	52.8	46.0	38.8	45.2	56.0	46.2	53.0	--	50.0	56.6
			(1.8)	(2.0)	(3.0)	(4.6)	(1.2)	(9.0)	(3.9)	(-)	--	(13.0)	(3.5)
		DT	25.3	25.0	34.2	29.5	25.8	27.0	28.2	30.0	--	25.5	29.4
			(.7)	(1.0)	(2.2)	(.5)	(1.5)	(3.0)	(1.2)	(-)	--	(1.5)	(.6)
		GR	2.08	2.13	1.36	1.32	1.78	2.14	1.67	1.77	--	2.00	1.92
			(.08)	(.12)	(.1)	(.16)	(.14)	(.57)	(.18)	(-)	--	(.62)	(.1)
	F	WT	84.9	71.0	71.0	70.1	72.6	73.3	85.5	90.0	--	82.5	80.0
			(3.0)	(4.1)	(5.9)	(2.3)	(9.0)	(8.0)	(17.5)	(-)	--	(4.1)	(5.2)

Table 4.8 cont'd

DT	27.3	29.6	32.4	31.5	30.9	29.0	35.0	30.0	--	27.4	31.0
	(.6)	(.8)	(1.7)	(.5)	(1.3)	(1.0)	(5.0)	(-)	--	(.4)	(1.0)
GR	3.12	2.43	2.23	2.23	2.43	2.55	2.57	3.00	--	3.03	2.59
	(.14)	(.19)	(.26)	(.09)	(.34)	(.37)	(.87)	(-)	--	(.17)	(.24)

Table 4.9: Analysis of OBL development time on four host species using a log-linear model.

SOURCE	d.f.	G	P
Family X time	46	152.72	< 0.001
Host X time	9	18.52	0.030
Sex X time	3	43.59	< 0.001
Family X sex X time	20	28.61	0.096
Host X sex X time	9	11.13	0.267
Host X family X time	50	96.13	< 0.001
Host X family X sex X time	2	8.56	0.381

Table 4.10: Analysis of variance on pupal weight (in mg) and egg-to-pupa growth rate (mg/day) in the OBL fed four different hosts.

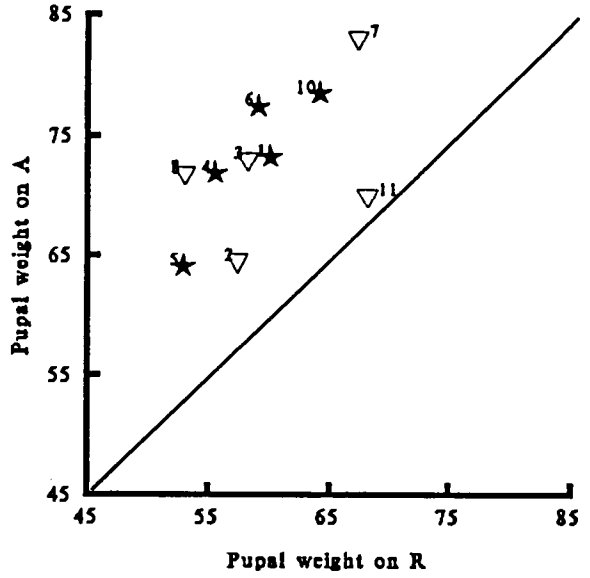
SOURCE	MS	d.f	DENOMINATOR MS	F	P
PUPAL WEIGHT [1]					
Family	658.68	10; 10.60	220.13	2.99	0.045
Host	2453.68	3; 51.16	109.35	22.44 [2]	---
Sex	58927.09	1; 13.53	182.73	322.48 [2]	---
Family X host	106.45	29; 29	85.49	1.24	0.279
Family X sex	201.14	10; 37.89	88.64	2.27	0.034
Host X sex	591.82	3; 57.34	93.22	6.35	0.0009
Family X host X sex	85.49	29; 335	119.05	0.72	0.859
EGG-TO-PUPA GROWTH RATE [3]					
Family	2.590	10; 15.48	0.577	4.49	0.0043
Host	2.791	3; 10.29	0.271	10.29 [2]	---
Sex	49.479	1; 13.79	0.401	123.51 [2]	---
Family X host	0.268	29; 29	0.114	2.36	0.012
Family X sex	0.437	10; 45.49	0.129	3.37	0.0023
Host X sex	0.870	29; 83.89	0.152	5.71	0.0013
Family X host X sex	0.114	29; 335	0.281	0.40	0.998

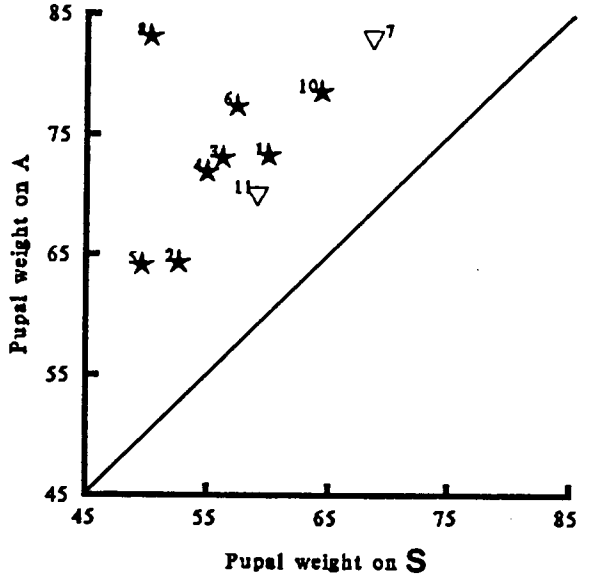
1 $r^2 = 0.75$
2 F tests not valid unless the Host X sex effect is assumed to be zero.
3 $r^2 = 0.61$

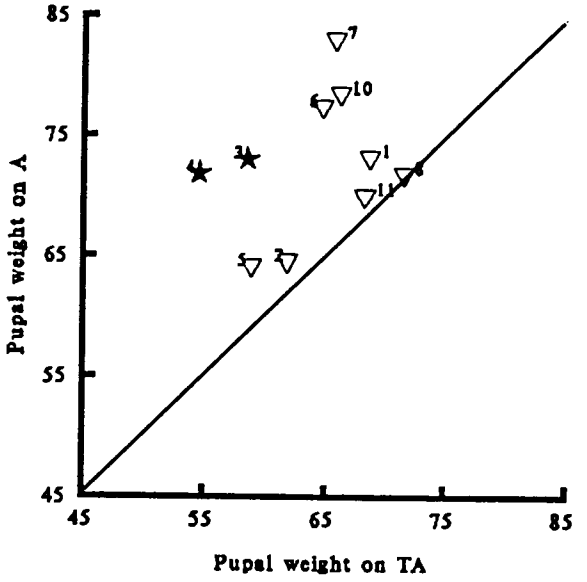
expectations. In this case, the other fixed effects have to be assumed to be zero for the test to be legitimate (SAS, 1988). However, approximate F tests of the Host and Sex effects conducted using the Family x host and the Family x sex effects as respective error terms were highly significant. The significance of the Host x sex effects for the two characters is probably due to the fact that males attained larger pupal size on A and TA than on R and S whereas females grew larger on A only (Chapter 2). The Family x sex term was significant in both cases, showing that the average response of the sexes to the four hosts was different among the families. This indicates that genetic variation was present in the amount of sexual dimorphism in PW and GR in the population studied.

The correlations in pupal weight attained on host-pairs are represented in Figure 4.2. Since they were estimated from the LSM computed for every combination of Family x host, the significant Sex, Family x sex and Host x sex effects were averaged and do not influence the values of the correlations. It was not possible to estimate the LSM for family 9, for which no observations were made on TA (Searle et al., 1980). For this reason, family 9 was excluded from the plots. Out of the ten remaining genotypes, five, eight and two attained a significantly higher pupal weight on A than on R, S and TA respectively. The proportion of the genotypes that performed better on A versus the other host was statistically different among the

Figure 4.2. Correlations of least square means in pupal weight attained on host pairs. Families represented by stars performed significantly better on A than on the other hosts, whereas families represented by triangles did not differ in their feeding performance on the two hosts. Lines of equal feeding performances on the host pairs are represented. The host pairs are a) A - R, b) A - S and c) A - TA.


85
75
65
55
45
45
55
65
75
85
Pupal weight on A
Pupal weight on R

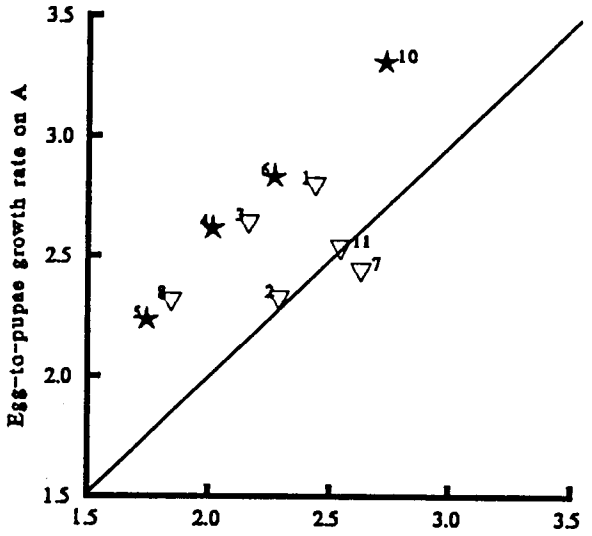

85
75
65
55
45
45
55
65
75
85
Pupal weight on A
Pupal weight on S

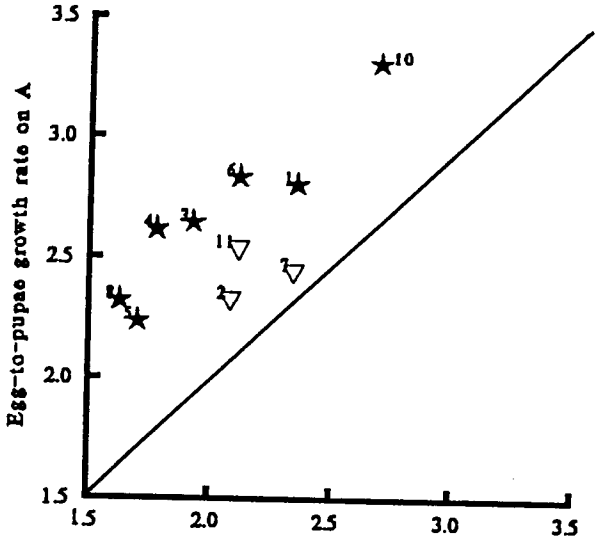

85
75
65
55
45
45
55
65
75
85
Pupal weight on A
Pupal weight on TA

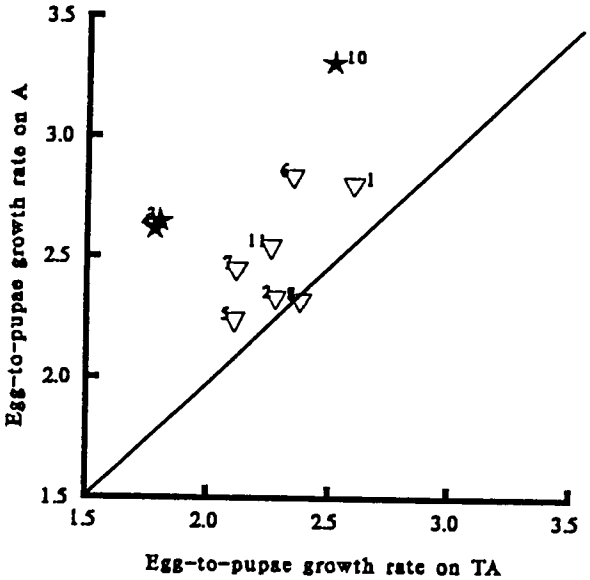
host-pairs (X^2 = 7.2, df = 2, P = 0.027), suggesting that TA and A were nutritionally more similar than R and S to the insects. The LSM method allows one to visualize the degree of specialization that was present among the families. For example, insects from family 4 performed significantly better on A than on the three other hosts, and could be categorized as specialists on A. On the contrary, insects from families 7 and 11 did not perform better on A than on any of the hosts, and would be more appropriately classified as generalists. Out of the remaining seven families, five and two performed significantly better on A than on two and one of the three alternative hosts, respectively. The Bonferonni procedure resulted in conservative tests (the level of acceptance for a significant difference between pairs of LSM was P = 0.0033). Thus, some of the families which appeared to perform better on A than on the other hosts were not designated as specialists by the tests (for example, family 7).

Similarly, four, seven and three of the genotypes had a significantly higher egg-to-pupa growth rate on A than on R, S and TA respectively (Figure 4.3). The difference among the proportion of specialized versus generalized genotypes on the host-pairs was not statistically different, however (X^2 = 3.482, df = 2, P = 0.175). Following the previous classification, families 4 and 10 were specialists, 2, 7 and 11 generalists, and two of the remaining families each

Figure 4.3. Correlations of least square means in egg-to-pupa growth rate attained on host pairs. Families represented by stars performed significantly better on A than on other hosts, whereas families designed by triangles did not differ in their feeding performance on the two hosts. Lines of equal feeding performances on the host pairs are represented. The host pairs are a) A - R, b) A - S and c) A - TA.


Egg-to-pupae growth rate on A
Egg-to pupae growth rate on R
3.5
3.0
2.5
2.0
1.5
1.5
2.0
2.5
3.0
3.5


Egg-to-pupae growth rate on A
Egg-to-pupae growth rate on S
3.5
3.0
2.5
2.0
1.5
1.5
2.0
2.5
3.0
3.5


Egg-to-pupae growth rate on A
Egg-to-pupae growth rate on TA
3.5
3.0
2.5
2.0
1.5
1.5
2.0
2.5
3.0
3.5

performed significantly better on A than on two and one of the three alternative hosts respectively.

The overall genetic correlations in PW and GR measured on host-pairs were all positive (Table 4.11). Unit normal correlations between pupal weight and development time were negative for both sexes ($r = -0.499$, $P = 0.0027$, $n = 34$ for males; $r = -0.543$, $P = 0.0019$, $n = 30$ for females), indicating that families attaining a high relative pupal size on a host also had relatively fast growth rates on that same host. However, the correlations in PW and GR measured on host-pairs were negative when potential general vigor and/or maternal effects of the genotypes were corrected (Table 4.11), suggesting that feeding trade-offs were present in the population studied.

DISCUSSION

The main objective of this experiment was to measure the genetic correlation between fitness components expressed on different hosts to determine whether feeding trade-offs were present in the OBL and to gain information on the ubiquity of genetically-based feeding trade-offs in herbivorous insects. If abundant, such trade-offs could then be considered when elucidating why the majority of phytophagous insects species are specialized in host use.

Most least squares means in feeding performance were located above the line of equal feeding performance on the host-pairs, indicating obliquebanded leafrollers had evolved

Table 4.11: Genetic correlations in A. pupal weight and B. egg-to-pupa growth rate attained on the four hosts. The genetic relationships were estimated from Least-square means for each combinations of Family X host (above the diagonal) or from corrected Least-square means ($LSM_{Family\ X\ host} - LSM_{Family}$; below the diagonal).

A. PUPAL WEIGHT [1]	Apple	Rose	Snowberry	Trembling aspen
Apple	--	0.576	0.838 ***	0.306
Rose	- 0.629 *	--	0.869 ****	0.282
Snowberry	0.266	0.314	--	0.433
Trembling aspen	- 0.466	- 0.326	- 0.902 ****	--

B. EGG-TO-PUPA GROWTH RATE	Apple	Rose	Snowberry	Trembling aspen
Apple	--	0.740 ***	0.670 **	0.350
Rose	- 0.454	--	0.793 ***	0.398
Snowberry	0.092	0.225	--	0.529
Trembling aspen	- 0.392	- 0.581 a	- 0.569 a	--

[1] * P = 0.052, ** P < 0.05, *** P < 0.01, **** P < 0.001.
a P < 0.09

a high feeding performance on apple (Figure 4.2 and 4.3). The results also suggest that genetic variation in feeding specialization on apple was present within this population. However, the overall family mean correlations in the feeding performance traits measured on host-pairs were all positive and did not provide evidence that a higher feeding performance on apple resulted in a lower performance on other hosts. Instead, the overall patterns of the correlations suggest that a substantial proportion of the alleles conferring a high feeding performance on one host also provided a high feeding efficiency on the other hosts, as would be expected in truly generalized insects (*sensu* Via, 1984b, 1987, Futuyma and Philippi, 1987).

These positive genetic correlations could be due to an artifact of the laboratory environment and/or to maternal effects. If this supposition is valid, the family mean correlations in the values of the fitness parameters expressed on the host-pairs should be corrected to accurately reflect the magnitude of feeding trade-offs. When such corrections were performed, evidence for the presence of a trade-off in the propensity to diapause on bushes versus trees was found. The fact that trees were nutritionally different from bushes to the obliquebanded leafrollers is supported by the estimates of larval growth rates (Table 4.6) and the significant difference in the proportion of the specialized and generalized genotypes observed on the host-pairs (Figure 4.2). To the extent that

the incidence of diapause in the offspring of an individual influences its genetic contribution to future generations, diapausing propensity may be considered as a fitness component. At the beginning of the summer, a newly hatched larva has two options: it can either diapause and resume feeding in the next spring, or develop to adulthood and leave offspring that will diapause in the fall. In a stable environment, the stategy producing the greater number of diapausing larvae resuming feeding in next spring would be expected to spread in a given population. However, when the benefit of these strategies reverses from season to season in an unpredictable manner, it can be shown theoretically that a mixed diapausing strategy will result in a greater mean reproductive rate than a pure strategy (Lomnicki, 1988). Therefore, a trade-off in the diapausing responses on bushes versus trees could slow the evolution of the optimal norms of reaction in the incidence of diapause on different host species within a given population, and promote the exclusive use of either bushes or trees.

The corrected family mean correlations in pupal weight and adult growth rate also provided evidence that feeding trade-offs existed within this population. Therefore, under the assumptions that general vigor or maternal effects influenced the traits, this study, along with other work (Gould, 1979, Futuyma and Philippi, 1987, Fry, 1990, Via, 1991), provides evidence of the existence of feeding trade-offs within populations of phytophagous insects.

A major assumption in this experiment is that the pattern of genetic correlations in feeding performance on host-pairs was mainly due to pleiotropic or linkage disequilibrium effects influencing the insect's detoxification efficiency. Since feeding efficiency was not estimated directly, it is possible that the feeding trade-offs resulted from differences in larval feeding rates or preferences instead of differences in detoxification efficiencies. Although this would change the nature of the feeding trade-offs, it would not modify their evolutionary consequences.

It is very interesting to note that adult size was similar in the laboratory and the field, which suggests that the rearing conditions did not influence OBL growth. However, similar phenotypic means attained in two environments does not preclude the possibility that a Family x environment (laboratory) interaction biased the values of the genetic correlations (Via, 1984a).

Raising the sibs in groups may have inflated the "family" component through common environment effects. Other potential sources of bias of the genetic parameters are maternal or non-additive genetic effects. The influence of non-additive effects on the values of the genetic correlations can still be considered as part of a feeding trade-off (Via, 1984b). Since all parents producing the sib-groups had thrived on apple leaves, it was assumed that maternal influences on the insect phenotype would be

minimal, and that the genetic parameters would represent broad sense estimates. However, further experiments on this population demonstrated that maternal effects can influence offspring phenotype, as well as the rank order in the mean phenotype of specific families for some traits (Chapter 5). Therefore, "family" effects may be inflated by non-genetic maternal influences and the values of the genetic correlations have to be considered cautiously. More specifically, a Maternal effect x family x host interaction could possibly have contributed to the variation in specialization among the genotypes (Figures 4.2 and 4.3). Again, such an interaction would change the nature of the feeding trade-offs, but not their evolutionary consequences.

Patterns of genetic correlation between pairs of life-history characters expressed on the same host have been found to vary on different hosts in herbivorous insects (Via, 1984 b, Pashley, 1988, Karowe, 1990). The significance of the across-host correlations between the characters in this study suggests that the genetic correlations are less labile than has been previously found in other insects. There was evidence for a positive genetic correlation between larval live weight and adult fitness, suggesting that selection for fast larval growth rates would result in a correlated increase in pupal size, and in a decrease in adult development time. However, there was evidence for a negative genetic correlation between diapausing propensity, larval growth rate and adult

development time. This suggests that a selective increase in the propensity to diapause in the summer could result in slower larval growth and longer adult development time. This could indicate the existence of a trade-off between achieving an optimal diapausing propensity and maintaining high growth rates in this population.

Although the sample size in this experiment was small, the distribution of diapausing intensities observed here appeared bi-modal. This could indicate that 1) disruptive selection produced two "types" of insects, one expressing a low and the other a high diapausing propensity in the summer or, 2) maternal effects accounted for the bimodality in diapausing intensities. The maintenance of the two "types" would depend on the equality of their genetic contributions to future generations and on the degree of reproductive isolation maintained between them. Alternatively, maternal effects could have arisen because the adults producing the insects used in this experiment developed under different conditions (Chapter 5). The full-sib design used in this experiment does not allow one to weigh the importance of genetic versus maternal effects in producing the pattern of diapausing intensities.

Implications of using a comparative method to detect feeding trade-offs. As for the comparisons of feeding performance between different species that are confounded by the effect of divergent selective pressures, the within population

measurement of genetic correlations in feeding performance traits may reflect the effect of alleles not directly influencing feeding efficiency. In the present experiment, evidence for the presence of feeding trade-offs was found when presumed general vigor and/or maternal effects were corrected for. The only experiment conducted simultaneously in the laboratory and in the field (partially) reported similar positive correlations between live larval weight measured on different hosts in both cases (Futuyma and Philippi, 1987). This suggests that general vigor effects did not bias the values of the genetic correlations in feeding performance in that species. Field experiments are needed to investigate whether feeding trade-offs are a dominant factor affecting the patterns of genetic correlations in feeding performances.

An alternative explanation for the relative rarity in herbivorous insects of negative genetic correlations in a single feeding performance trait expressed on different hosts may be that many performance traits covary in a similar manner across the hosts. For example, a genotype attaining a relatively large pupal size and having long development time on all the hosts used within a population may have similar fitness as another genotype developing relatively faster but producing smaller adults on every host. Unless strong feeding trade-offs were present to oppose these antagonistic relationships between characters, the across-host genetic correlations measured in a single

trait influenced by such antagonistic pleiotropy would be positive. Since it is possible that antagonistic pleiotropy does exist between major fitness components in herbivorous insects (Smith et al., 1987, Holloway et al., 1990), even small trade-offs that would be undetected by measuring genetic correlations in feeding performance in a single trait expressed on different hosts, could have an impact on the evolution of host use in phytophagous insects.

Unless feeding trade-offs are the dominant factor that affects the patterns of genetic correlation on different hosts, selection experiments will be more appropriate than measurement of within population genetic correlations to detect their presence (Fry, 1990). Attempts to detect feeding trade-offs in the field should either involve measuring total fitness (Via, 1991), or at least estimate many fitness components on many hosts, such that potential antagonistic relationships between fitness components could be detected, and considered when measuring genetic correlations in a single trait expressed on different hosts.

CONCLUSION

The detection of negative genetic correlations in pupal weight and egg-to-pupa growth rate on pairs of host species, and of an inverse genetically-based propensity to diapause on bushes versus trees, supports the hypothesis that host specialization reduces the ability to efficiently use different hosts in the obliquebanded leafroller. These

trade-offs were only apparent when the potential influences of general vigor and/or maternal effects were statistically eliminated. Many of the previous studies conducted to investigate the commonness of feeding trade-offs in herbivorous insects did not control for the potential impact of antagonistic pleiotropy, maternal effects, or general vigor, on the values of the genetic correlations in feeding performance on host-pairs. Therefore, it is possible that the trade-off hypothesis has not been adequately tested to date.

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Chapter 5:

MATERNAL INFLUENCES ON LIFE HISTORY TRAITS IN THE OBLIQUEBANDED LEAFROLLER

SUMMARY

The influence of maternal effects on the phenotypic mean, variance and heritability of feeding performance traits and diapausing propensity was investigated in the obliquebanded leafroller. Three successive generations were raised on an artificial diet in a constant environment. The main difference between the generations was in the origin of the parents, as the first and subsequent generations originated from field and laboratory parents, respectively. Assuming that changes in gene frequency were minimal from generation one to three, the between-generation differences in phenotypic means, variances, and heritabilities were attributed to changes in maternal effects.

The results suggest that maternal effects influenced the mean diapausing propensity among families, pupal weight, and development time, but did not influence larval live weight. Phenotypic variance was greater in most characters when offspring originated from field than from laboratory parents. Parent-offspring heritabilities of diapausing propensity derived using parental values from the first generation were highly significant and similar to parent-offspring heritabilities derived using parental values from the second generation. However, parent-offspring heritabilities of live larval weight were not significant

when first-generation parental values were used as regressors. This is contrary to the significant parent-offspring heritabilities obtained when parental values from the second generation were used. Parent-offspring regressions using first-generation parents were significant and non-significant for development time and pupal weight, respectively. When parents were reared in the laboratory, parent-offspring or full-sib estimates revealed that all traits were heritable. The different impact of maternal influences of field mothers on the parent-offspring heritabilities of the traits (derived using first-generation parents), may be due to the influence of diverse maternal effects on each character, or to different responses of the traits to the same maternal effect.

As when insects were fed on host plants (Chapter 4), the genetic correlations between diapausing propensity within a family and larval live weight or development time were negative and positive, respectively. The stability of these genetic relationships suggests that the joint evolution of rapid development and high diapausing propensity may be constrained in this species.

INTRODUCTION

Heritabilities and genetic correlations are estimated in breeding experiments that partition the total observed phenotypic variance and covariance into additive genetic components versus non additive and environmental deviations (Falconer, 1981). Maternal effects, which are developmental influences transmitted by the mother to her offspring, contribute to the environmental variance component of these measurements and reduce the precision of the genetic estimates (Mousseau and Dingle, 1991). Unless a half-sib design is used to extract the additive components of variance and covariance, it is necessary to assume that such estimates are not influenced by maternal effects.

One of the major questions remaining from the experiments in Chapter 4 was whether maternal effects could have biased the values of the genetic parameters estimated using a full-sib design. Since all the parents producing the full-sib groups developed on the same host, it was assumed that environmentally induced variation in maternal effects was minimized. However, I found that a considerable proportion of the larvae initiated diapause in the summer (Chapters 2 and 4). The parents may therefore have developed from larvae that had initiated diapause either at the beginning of the previous summer, or later in the fall. Moreover, diapause was initiated in different larval instars (Chapter 2). Differences in diapausing conditions may result in variation in larval physiology that could be

transmitted to the adults and lead to differences in maternal effects. Consequently, I decided to investigate whether maternal effects influence offspring development in the obliquebanded leafroller (OBL).

Variation in maternal effects influencing offspring development may be due to genetic or environmental differences in the maternal generation (Mousseau and Dingle, 1991). Assuming additivity of the sources of variation that contribute to maternal effects, the environmental component of variance transmitted by the mother to her offspring can be expressed as: $V_{pm} = V_{gm} + V_{em} + V_{gm \times em} + V_e$, where V_{gm} is the genotypic variance in maternal effects (due to additive and non-additive genetic variance), V_{em} is the variance arising from the mothers' average responses to each environment, $V_{gm \times em}$ is the variance generated by unequal responses of the genotypes to different environments and V_e is the error variance. The contribution of the V_{em} and $V_{gm \times em}$ terms is expected to be greater when the mothers developed (or diapaused) in different rather than in homogeneous environments. Accordingly, the phenotype of mothers and offspring raised in a constant environment are expected to be less correlated when the grandmothers have been raised in different rather than similar environments.

The experimental approach used to detect maternal effects consisted of raising three consecutive generations of obliquebanded leafrollers in a controlled environment and deriving heritabilities using both full-sib and parent-

offspring estimates. The first generation originated from parents collected in the field. The two subsequent generations were derived from parents sampled from the previous, laboratory raised generation. A large number of families were sampled to establish each generation and mortality due to rearing conditions was negligible. Therefore, I assumed that changes in gene frequency were minimal from generation one to three (see Materials and Methods). Consequently, variation in phenotypic means, variances and heritabilities between the first and the two subsequent generations could be attributed to differences in maternal effects.

Four predictions can be made that would support the hypothesis that maternal effects are present in the OBL. First, a large environmental component of variance transmitted by field mothers should result in higher phenotypic variance in the first than in subsequent generations. Second, mean phenotypes should differ between the first and subsequent generations. Third, parent-offspring heritability estimates should be lower when the offspring had field collected grandmothers than when they had laboratory raised grandmothers. Finally, full-sib heritability estimates should be greater in the first than in subsequent generations, because maternal effects contribute to the covariation among offspring family means without affecting the within family phenotypic variance (Falconer, 1981).

MATERIALS AND METHODS

Source of insects and experimental design. Larvae in their last two instars were collected from the population described in Chapter 4 on two consecutive days at the end of May 1990. They were transferred to an artificial pinto bean diet (modified from Shorey and Hale, 1965) and raised individually in the laboratory under a 16 L: 8 D light regime and a 22.5 °C (day), 20 °C (night) temperature cycle. These conditions were used to raise all insects in this experiment.

Resulting adults were paired to yield 42 families of larvae that made up the first generation. Forty-two families were also raised in the second and third generations. To increase the precision of the estimates of heritability in diapausing propensity, the parents of the second and third generations were mated assortatively with respect to that trait. Sib matings were not permitted and a given female was never mated to more than one male. A family consisted of 30 larvae raised individually, always originating from the mother's first egg mass. Each family was placed as a group in a randomly chosen section of the growth chamber and every day, the groups were randomly re-located. The heritability estimates and genetic covariances may therefore have been biased by a common environment effect.

Measurement of fitness components. Sixteen days after the onset of feeding, the larvae that had not initiated diapause were weighed. At that time, the proportion of the surviving larvae in each family that had initiated diapause was recorded. A larva was considered in diapause if it had spun a cocoon within its cup, or if it was in the beginning of its third instar or smaller (at that time, most larvae were in their fifth or sixth instars). These latter larvae were transferred to plastic cups containing a piece of cardboard as a diapausing substrate. Sixty-eight percent successfully spun a cocoon and diapaused after being transferred. This is comparable to the diapausing incidence of the wandering larvae observed in Chapter 2 and suggests that the criteria used to designate diapausing larvae was adequate. Every day, all larvae were checked, new pupae weighed, and their total larval development time recorded.

Generation differences and maternal effects. To detect the influence of maternal effects on diapausing propensity, the distributions of within family diapausing incidence were compared between parents and second- and third-generation larvae. The distributions of within family diapausing propensities were also compared between the first experimental generation (produced by adults originating from larvae collected in the spring) and families produced by adults originating from larvae collected in the field at the beginning of August 1990. These latter larvae were

collected in their last two instars from the same orchard used to establish the first experimental generation. The spring and summer larvae normally contribute to the two successive flights observed in the field (Chapter 2). Changes in phenotypic means and variances in live larval weight after 16 days (LW), pupal weight (PW) and total development time (DT) were compared between successive generations.

Changes in gene frequencies among generations. Changes in gene frequency due to selection or random sampling of gametes in small populations have to be ruled out to attribute among-generation changes in phenotypic means, variances and heritabilities to variation in maternal effects. Without replication, it is not possible to establish with certainty that changes in gene frequency did not contribute to the variation in the parameters mentioned above. However, two types of indirect evidence support the role of maternal effects as a major source of variation in phenotypic means and variances in this experiment.

First, it is possible to predict the changes in mean phenotype in successive generations using the relationship $R = h^2 \times S$, where R is the predicted change in mean phenotype between two generations, h^2 is the heritability of the trait and S is the selection differential (Falconer, 1981). Since the heritability of a trait can not exceed 1, in the case where there is no non-genetic cause of variation, the

observed change in mean phenotype between two generations should not be greater than the selection differential. Larval survival (excluding the diapausing larvae) was around 98 % in the three generations and the selection differentials associated with mortality due to the rearing conditions are assumed to be negligible. R and S were calculated and compared for the three generations. Changes in mean phenotypes above S values would be indicative of the influence of maternal effects.

Second, under simplifying assumptions, it is possible to roughly predict the magnitude of the expected *average* change in means and variances that would result from random sampling of alleles among many isolated populations comparable in size to the experimental populations (Falconer, 1981). One of the simplifying assumptions necessary to conduct these estimations was violated in the experimental populations (i.e. mating was not random within the populations). The impact of assortative mating on the predictions was assumed to be negligible.

The average effect of random changes in gene frequency on the genotypic variance found within populations of similar size (lines), can be described as a function of the inbreeding coefficient (Falconer, 1981, p. 240). Assuming that the genetic variance is totally additive, the genotypic variance is expected to decrease proportionally to (1 - F) times the genotypic variance that was present in the base population, where F is the inbreeding coefficient of the

generation considered. The inbreeding coefficients were calculated for the second and third generations, adjusting for the observed unequal contribution of the families in breeding individuals to the next generation (Falconer, 1981, p. 66). Their values were 0.00846 and 0.01739 for the second and third generations, respectively. These small F values suggest that on average, the expected change in genotypic variance due to sampling error would be minimal over the first three generations (for example, assuming heritabilities of 1, mean changes in phenotypic variance would be around 1 % between the first and second generations). Still assuming that all the genetic variance is additive, the variance in the mean phenotypes in successive generations is expected to be equal to 2F times the genotypic variance that was present in the base population (Falconer, 1981, p. 241). Except perhaps for development time in males (the predicted variance in the means after one generation was 4.4 times smaller than the observed changes), the small F values suggest that on average, sampling effects would have little influence on the variation in the mean phenotypes observed in this experiment.

Experimental analysis and estimations of heritabilities. Diapausing intensities. Many characters vary in a discontinuous manner but are inherited as quantitative traits. The phenotypic expression of such "all-or-none"

traits is assumed to result from the interaction of an underlying continuous variable with a threshold: the observed phenotypes take one form or the other, depending upon whether the value of the underlying variable is below or above the value of the threshold (Falconer, 1981). As in classical determination of quantitative traits, the value of the underlying variable is influenced by a genetic and an environmental component. The threshold model has been found to describe successfully the inheritance of many characters of biological interest (see for example Roff, 1986, Tauber and Tauber, 1986).

The heritability of the incidence of diapause within families was estimated separately for each sex using a parent-offspring regression technique suitable for threshold characters (Roff, 1986). The heritability estimates were corrected for assortative mating using the formula given by Falconer (1981, p. 164); the phenotypic correlation between the parents that was found using this formula was calculated from parental values measured on the underlying continuous scale (i.e. using the probit transformed proportion of diapause observed within the families; see Roff, 1986, 1990).

Larval weight, pupal weight and development time. The significance of the family, sex and family x sex interaction was assessed for LW, PW and DT for the three generations using an analysis of variance. Type III sums of squares

were used and F tests were conducted using Satterthwaite approximations in the GLM statistical package (SAS, 1988). Full-sib and parent-offspring heritability estimates of the traits were obtained for each sex. Standard errors of the estimates were calculated according to Becker (1984).

Third generation OBL larvae were not raised to pupation. Thus, parent-offspring estimates could not be calculated for PW or DT using second generation parents, nor could full-sib estimates be obtained for these traits in the third generation. There was a significant phenotypic correlation in LW in the parents crossed to produce the third generation, despite the fact that they had not been mated assortatively with respect to this trait. The parent-offspring estimates of heritability in LW obtained using second generation parents were thus corrected for assortative mating as described above.

Genetic correlations. The experimental design enabled me to estimate family mean genetic correlations (Via, 1984) between pairs of traits for each sex among and within generations. Parent-offspring correlations are less likely to be biased by common environmental effects than full-sib correlations. Comparison of the correlations estimated using both methods permitted assessment as to whether common environment affected the within-generation estimates.

RESULTS

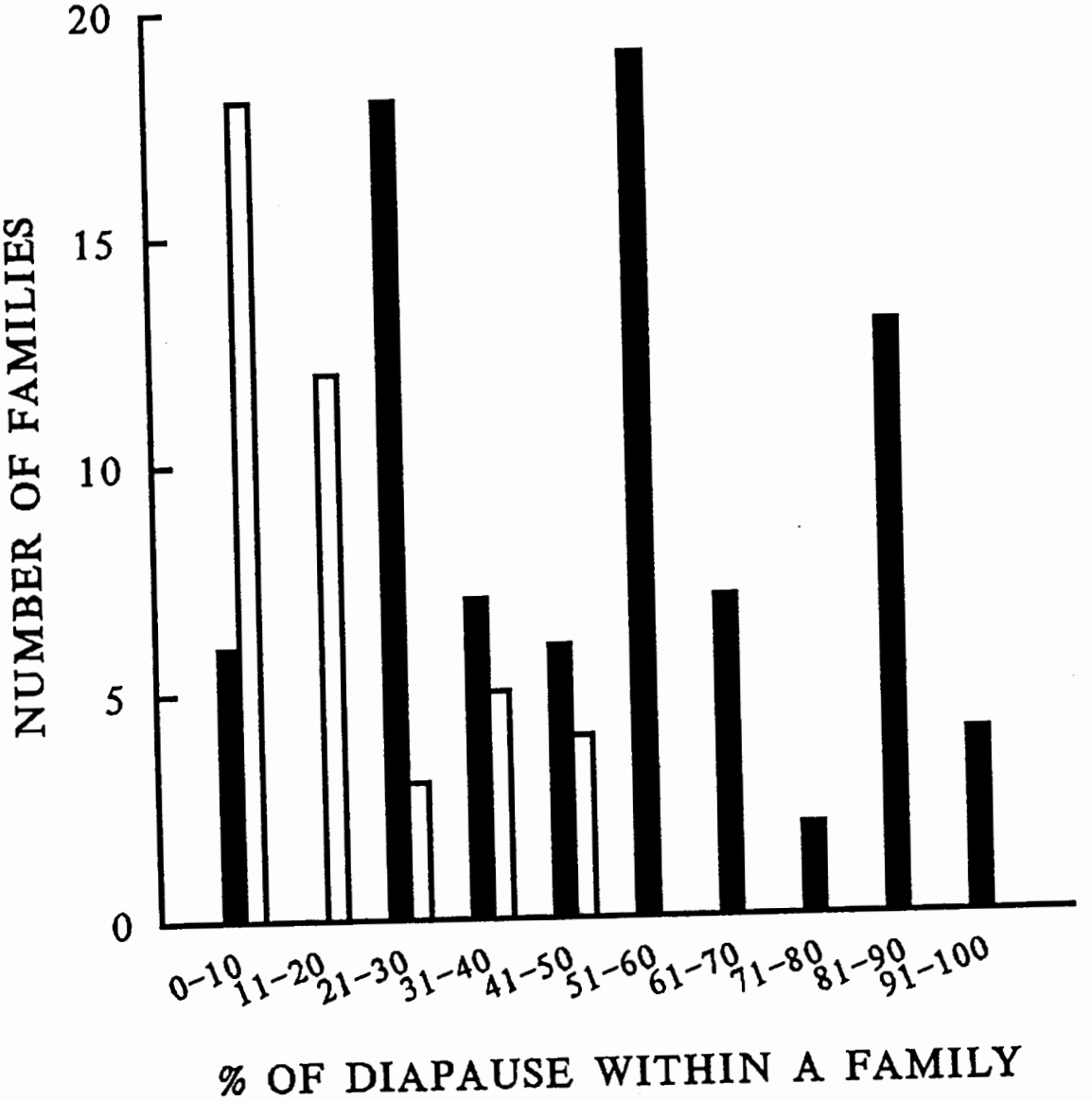
Generation differences and maternal effects. The mean incidence of diapause was evidently greater in the first than in subsequent larval generations (Table 5.1). The among-generation differences in the variance in diapausing propensity are difficult to interpret because the large changes in the mean phenotypes could have produced changes in the variances as a scale effect (Falconer, 1981). The mean diapausing propensity of the parental families crossed to produce the second generation and of their offspring were 0.52 ± 0.25 (± SD) and 0.17 ± 0.14, respectively. The distributions of diapausing propensities were statistically different between the two groups (Mann-Whitney, $U = 421$, $X^2 = 48.45$, $P < 0.001$; see Figure 5.1). However, the distributions of diapausing incidence of the parental families crossed to produce the third generation and of their offspring was similar ($U = 1500$, $X^2 = 1.88$, $P = 0.17$:Mean diapausing propensity in parents, 0.22 ± 0.18; 0.17 ± 0.13 in offspring). The observed change in diapausing incidence between the first and second generations, and the contrasting lack of change between the second and third generations, suggests that maternal effects influenced diapausing propensities in the first generation.

The mean diapausing propensity of larvae produced by spring and summer parents was 0.70 ± 0.24 and 0.38 ± 0.23, respectively. The two offspring groups had different

Table 5.1. Mean proportion of diapausing offspring (± SD) among the families raised for three generations in the laboratory.

	Generations		
	1	2	3
Proportion of diapause	0.70 (.24)	0.17 (0.14)	0.17 (0.13)

Figure 5.1. Distribution of diapausing propensities within the parental families used in the crosses to produce the second generation and within the 42 families raised in the second generation. Solid bars represent the parents; open bars their offspring.


20
15
10
5
0
NUMBER OF FAMILIES
0-10
11-20
21-30
31-40
41-50
51-60
61-70
71-80
81-90
91-100
% OF DIAPAUSE WITHIN A FAMILY

distributions of diapausing propensities ($U = 956.5$, $X^2 = 21.87$, $P < 0,001$; Figure 5.2), further indicating the impact of maternal effects on diapause incidence in the OBL. Since summer parents are more likely to have originated from families with a low propensity to diapause in the spring, it is possible that part of the reduction in the propensity to diapause between offspring originating from spring and summer parents had a genetic basis. However, the change in the distribution of the propensity to diapause between the offspring of spring and summer parents was similar to the change in distribution observed between the first and second laboratory generations. This latter change was unlikely to be due to a variation in gene frequency, which suggests that the shift in the mean propensity to diapause between offspring from spring and summer parents was mainly due to the influence of different maternal effects.

Mean live larval weight after 16 days, an index of larval growth rate, was not significantly different between offspring of field parents and the second generation originating from laboratory produced parents (Table 5.2). However, compared to second-generation offspring, field parents had offspring that attained higher PW in both sexes and male offspring that took less time to develop. Phenotypic variance was larger in the first than in the second generation for all traits except DT in males (Table 5.2). These results suggest that maternal effects transmitted by field mothers modified the phenotypic mean

Figure 5.2. Distribution of diapausing propensities within families originating from "spring" and "summer" field collected obliquebanded leafrollers. Solid bars represent offspring originating from "spring" parents; open bars, "summer" parents.

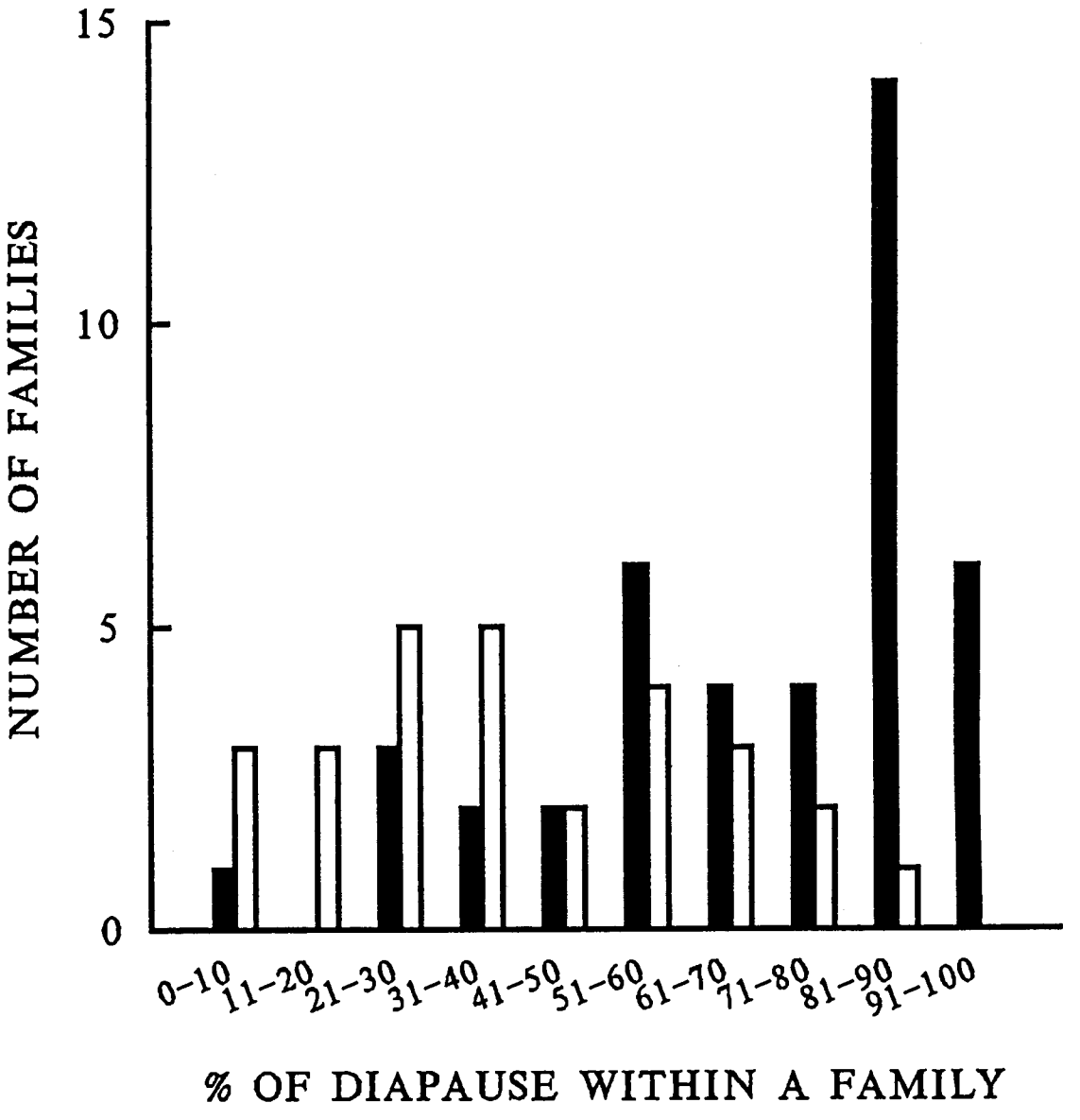

15
10
5
0
NUMBER OF FAMILIES
0-10
11-20
21-30
31-40
41-50
51-60
61-70
71-80
81-90
91-100
% OF DIAPAUSE WITHIN A FAMILY

Table 5.2. Live larval weight after 16 days (LW; in mg, ln transformed), pupal weight (PW; in mg, ln transformed) and development time (DT; in days) for three generations of OBL raised in the laboratory. Means (X), standard deviations (SD) and sample size (N) are listed by sex.

			Generations				
Sex	Trait	Parameter	1		2		3
M	LW	X	4.27	NS[1]	4.32	*	4.56
		SD	0.82	*[2]	0.62	NS	0.65
		N	197		507		506
	PW	X	4.31	*	4.27		-
		SD	0.14	*	0.12		-
		N	198		510		-
	DT	X	21.8	*	22.3		-
		SD	2.6	NS	2.4		-
		N	197		510		-
F	LW	X	4.46	NS	4.50	*	4.71
		SD	0.84	*	0.61	*	0.72
		N	162		503		488
	PW	X	4.95	*	4.84		-
		SD	0.19	*	0.14		-
		N	162		500		-
	DT	X	24.1	NS	24.3		-
		SD	2.6	*	2.2		-
		N	162		503		-

[1] Satterthwaite approximate t-test of equality of means between generations (* = $P < 0.05$, NS = $P > 0.05$)

[2] Folded form of the F statistics to test for homogeneity of variances between generations (* = $P < 0.05$, NS = $P > 0.05$)

and variance in the offspring. Contrary to the first two generations, LW increased significantly between the second and third generations in both sexes. The phenotypic variance also increased in females (Table 5.2). The cause of these changes is unclear and may be related to undetected changes in the rearing conditions.

Changes in gene frequencies among generations. Selection differentials which differ from zero in Table 5.3 reflect the amount of "sampling error" that occurred when parents were selected to generate a subsequent generation. For all characters showing a significant change in mean phenotype between the first and second generations, the observed changes greatly exceeded, and often were in the opposite direction, of the selection differentials. The similarity of the mean LW between the first and the second generations suggests that changes in mean phenotypes were not due to variation in the rearing conditions. Thus, the changes in offspring phenotypes indicate that maternal effects transmitted by field mothers influenced first generation phenotypes. The observed change in LW between the second and third generations also exceeded the selection differentials. This shift in mean LW could have been due to undetected changes in the rearing conditions.

Impact of maternal effects on heritabilities. Although maternal effects influenced the mean incidence of diapause

Table 5.3. Selection differential and observed change in the mean phenotype of offspring for generations 1, 2 and generations 2, 3. The characters are live larval weight after 16 days (LW), pupal weight (PW) developmental time (DT) and propensity of diapause within a family (DIAP). The parameters are given by sex for LW, PW and DT.

Sex	Character	Selection differential	Observed change in offspring phenotype [1]
Generation 1, 2			
M	LW	+ 0.02	+ 0.05
	PW	+ 0.01	- 0.04 *
	DT	- 0.20	+ 0.50 *
F	LW	+ 0.06	+ 0.04
	PW	- 0.02	- 0.11 *
	DT	- 0.17	+ 0.20
	DIAP	- 0.18	- 0.53 *
Generation 2, 3			
M	LW	- 0.01	+ 0.22 *
F	LW	+ 0.03	+ 0.21 *
	DIAP	+ 0.05	0

[1] Characters which showed a significant change in mean phenotype between the two generations (from Table 5.2 and see Results for tests of DIAP)

in the first generation, parent-offspring heritability estimates derived using first-generation parental values were high (Table 5.4). This suggests that the field conditions generating maternal effects influenced all females equally, in which case the phenotype of first-generation larvae (the parents in the regressions) would reflect their breeding values. Regressions using either male or female second-generation parental values yielded similar heritability estimates as when mid-parental values were used, as expected if parents contribute equally to offspring phenotypes (Falconer, 1981). This suggests that heterogeneity in the laboratory conditions did not result in maternal effects influencing diapausing incidence.

Parent-offspring heritability estimates in LW derived using first-generation parental values were not statistically significant, except for the regression of female offspring on female parent (Table 5.5). However, estimates calculated using second-generation parental values were highly significant. This suggests that heterogeneity in the field conditions resulted in variation in maternal effects that reduced the correspondence between the phenotype and breeding value of first-generation parents. The similar heritabilities obtained when either second-generation male or female parental values were used as the regressor, again suggest that heterogeneity in the laboratory environment did not result in maternal effects influencing larval growth.

Table 5.4. Heritability estimates (± SE) for within family propensity of diapause, derived from regressions of offspring family means on single or mid-parent family means.

Generations	Regression	h^2 [1]
1, 2	On male parent	0.67 ± 0.21
1, 2	On female parent	0.60 ± 0.23
1, 2	On mid-parent	0.65 ± 0.14
2, 3	On male parent	0.48 ± 0.21
2, 3	On female parent	0.57 ± 0.15
2, 3	On mid-parent	0.53 ± 0.12

[1] All regression coefficients significant at $P < 0.01$

Table 5.5. Heritability estimates (± SE) for live larval weight attained after 16 days, derived from regressions of offspring on one parent, calculated separately for each sex.

Generations	Offspring	Parent	
		Male	Female
1, 2	Male	0.24 ± 0.13	0.15 ± 0.17
1, 2	Female	0.20 ± 0.17	0.28 ± 0.13* [1]
2, 3	Male	0.54 ± 0.16***	0.52 ± 0.15**
2, 3	Female	0.65 ± 0.13***	0.47 ± 0.16***

[1] Significance of the regression coefficient * $P < 0.05$, ** $P = 0.0003$, *** $P < 0.0001$

Parent-offspring estimates of heritability in PW and DT derived using first-generation parents are combined in Table 5.6 for convenience. Heritabilities in PW were not significant but parents that had short DT also produced offspring which developed rapidly (Table 5.6). Full-sib estimates for both traits were significant in the second generation, indicating that heritable variation in the traits was present in the populations (see below). Thus, the non-significant parent-offspring regression in PW was apparently not due to a lack of additive genetic variance in that trait. This suggests that the correspondence between the phenotype and breeding values of PW and DT in first-generation parents was influenced differently by variation in maternal effects.

Larval live weight, PW and DT all exhibited significant between-family variation in the three generations (Table 5.7). The sex effect was also highly significant in all but one case and there were some significant family x sex interactions, indicating that genetic variation in sexual dimorphism was present for some traits within the populations. Full-sib heritability estimates were significant for all traits in each generation (Table 5.8). Most heritability estimates were not statistically different between the first and second generation (Table 5.8). However, heritabilities in females tended to be larger in the first than in the other generations, indicating that maternal effects influenced the

Table 5.6. Heritability estimates (± SE) for pupal weight (PW) and developmental time (DT), derived from regressions of offspring on one parent, calculated separately for each sex. Parents originated from the first laboratory generation

Character	Offspring	Parent	
		Male	Female
PW	Male	0.27 ± 0.15	0.24 ± 0.16
	Female	0.22 ± 0.12	0.22 ± 0.13
DT	Male	0.55 ± 0.23*[1]	0.28 ± 0.15
	Female	0.54 ± 0.20*	0.44 ± 0.17*

[1] Significance of the regression coefficients: * = $P < 0.025$.

Table 5.7. Results of analysis of variance for live larval weight after 16 days (LW in mg, ln transformed), pupal weight (PW in mg, ln transformed) and developmental time (DT) for three generations of OBL

Generation	Source	LW		PW		DT	
		d.f.	F	d.f.	F	d.f.	F
1	Family	38; 33.34	2.92**[1]	38; 33.93	4.29**	38; 33.72	2.77**
	Sex	1; 60.26	0.17	1; 64.82	882.65**	1; 60.62	76.82**
	F x S	29; 290	1.24	29; 291	1.10	29; 290	1.23
2	Family	41; 41	3.94**	41; 41	2.94**	41; 41	6.43**
	Sex	1; 43.05	17.53**	1; 42.60	3188.13**	1; 43.17	192.68**
	F x S	41; 926	1.48*	41; 926	1.89**	41; 929	1.39
3	Family	40; 40	4.69**	-	-	-	-
	Sex	1; 41.59	11.15**	-	-	-	-
	F x S	40; 912	1.43*	-	-	-	-

[1] * = P < 0.05, ** = P < 0.001

Table 5.8. Estimates of heritability from full sibs (± SE) for live larval weight after 16 days (LW), pupal weight (PW) and development time (DT) calculated for each sex over 3 generations (Gen).

Sex	Gen	Character [1,2,3]		
		LW	PW	DT
M	1	0.52 ± 0.15 a	0.46 ± 0.15 a	0.38 ± 0.15 a
	2	0.41 ± 0.10 a	0.45 ± 0.10 a	0.57 ± 0.11 b
	3	0.42 ± 0.10 a	-	-
F	1	0.60 ± 0.17 a	0.68 ± 0.18 a	0.77 ± 0.18 a
	2	0.37 ± 0.09 a	0.35 ± 0.09 a	0.47 ± 0.11 a
	3	0.37 ± 0.10 a	-	-

1 F tests of full-sib components of variance all significant at $P < 0.0003$

2 Heritabilities followed by the same letter (within sex and columns) are not statistically different, 1 tailed F tests calculated from the ratio of the family mean squares

3 Heritabilities of PW and DT not calculated in the third generation since the larvae were not raised to pupation.

traits in females. Parent-offspring heritabilities of LW calculated using second-generation parents (Table 5.5) were significantly larger than the full-sib heritabilities estimated for the second and third generations (Table 5.8; $t = 3.795$, $df = 6$, $P = 0.009$). Full-sib heritability estimates are more likely to be inflated by common environment than parent-offspring estimates. The lower full-sib heritabilities suggest common environment was not a major source of variation in LW.

Within-generation correlations. Family mean correlations between LW and DT were strongly negative in the first two generations in both sexes (the four r_m had values between -0.87 and - 0.89, all $P < 0.0001$). The few other correlations between pairs of different traits that were significantly different from zero included DIAP as one of the traits (Table 5.9).

Between-generation correlations. The only significant correlations between pairs of different traits were found between first-generation female parents and their female offspring and included DIAP as one of the traits (Table 5.10). The highly significant correlations between LW and DT were not detected in between-generation correlations. This suggests that the relationships estimated using within-generation correlations were biased by common environment effects. Overall, the within- and across-generation

Table 5.9. Family mean correlations estimated separately for each sex within each generation (Gen) between mean values of diapausing propensities (DIAP) and larval weight (LW), pupal weight (PW) or development time (DT).

Gen	Sex	Character correlated with DIAP[1]		
		LW	PW	DT
1	F	-0.33 (0.118)	-0.016 (0.943)	0.32 (0.130)
1	M	-0.35 (0.075)	-0.16 (0.418)	0.39* (0.045)
2	F	-0.15 (0.353)	-0.34* (0.026)	0.10 (0.521)
2	M	-0.36* (0.021)	-0.24 (0.124)	0.24 (0.124)
3	F	-0.22 (0.175)	-	-
3	M	-0.26 (0.099)	-	-

[1] Values in parentheses are the probabilities that $r_m = 0$.
* = $P < 0.05$.

Table 5.10. Family mean correlations between mean parental and offspring values of larval weight attained after 16 days (LW), pupal weight (PW), development time (DT) and within-family diapausing propensities (DIAP). The correlations were estimated separately for each sex.

Sex	Parental Character	Offspring character[1,2] LW	PW	DT	DIAP
Generations 1, 2					
F	LW	0.19 (0.255)	0.13 (0.457)	-0.20 (0.235)	-0.27 (0.113)
	PW	-0.16 (0.357)	0.34* (0.044)	0.23 (0.179)	0.06 (0.741)
	DT	-0.12 (0.469)	0.08 (0.654)	0.21 (0.215)	0.31 (0.068)
	DIAP	-0.38* (0.016)	-0.11 (0.497)	0.44* (0.005)	0.49* (0.001)
M	LW	0.16 (0.367)	-0.03 (0.844)	-0.19 (0.285)	-0.11 (0.530)
	PW	-0.04 (0.807)	-0.21 (0.237)	-0.09 (0.603)	0.13 (0.461)
	DT	-0.24 (0.178)	0.15 (0.412)	0.33 (0.055)	0.06 (0.753)
	DIAP	-0.29 (0.065)	0.11 (0.499)	0.23 (0.146)	0.60* (0.0001)
Generations 2, 3					
F	LW	0.45* (0.005)	--	--	-0.07 (0.690)
	DIAP	-0.17 (0.311)	--	--	0.62* (0.0001)
M	LW	0.49* (0.002)	--	--	-0.28 (0.089)
	DIAP	-0.26 (0.119)	--	--	0.38* (0.019)

1 Values in parentheses are the probabilities that $r_m = 0$. * = $p < 0.05$

2 Pupal weight and development time were not measured in the third generation and the family mean correlations including these traits could not be calculated.

correlations suggest that there was a negative genetic correlation between DIAP and LW and a positive correlation between DIAP and DT.

DISCUSSION

Maternal effects are a form of phenotypic plasticity in which maternal influences on the environment of their progeny affect offspring phenotypic response (Mousseau and Dingle, 1991). Phenotypic plasticity can influence traits independently within the same organism (Schlichting, 1986). This facilitates the evolution of optimal responses of many traits in variable environments. The independence of responses can arise because the characters react differently to similar environmental conditions, or are influenced by distinct conditions.

The results of this study strongly suggest that maternal effects influenced the mean diapausing propensity within the families. It also appears that maternal effects influenced pupal weight and development time, but did not modify larval live weight, an index of growth rate. The parent-offspring heritability estimates for diapausing propensity were similar when values of mothers raised in the field or the laboratory were used as regressors. Therefore, mothers raised in the field and the laboratory transmitted different maternal effects to their offspring, but all mothers developing in a given environment appeared to be influenced similarly by the conditions inducing the maternal

effects. However, larval live weights seemed to be subjected to a greater variation in maternal effects in offspring of field mothers than in offspring of laboratory mothers. Consequently, the parent-offspring heritability estimates were influenced by the environment from which the mothers originated. Maternal effects of field mothers apparently influenced equally the development time of their offspring, but inflated the environmental variation influencing offspring pupal weight.

The different impact of the maternal influences on the heritability of the characters may indicate that distinct maternal effects influenced each trait. The population sampled to produce the first generation was composed of insects that had diverse diapausing histories (e.g. larvae had initiated diapause in the summer or the fall). First generation mothers may therefore have been divided into two or more "groups", each transmitting a distinct value of maternal effect to their offspring. However, first generation mothers also shared similar developmental conditions (e.g. all diapausing larvae resumed feeding in the spring), and in other respects may have transmitted similar maternal effects to their offspring. Therefore, it is possible that diapausing propensity and development time were influenced by maternal effects of similar value for all first generation larvae, whereas larval and pupal weight were influenced by maternal effects that varied discontinuously. Alternatively, the traits may

have been influenced by the same maternal effect in all first generation larvae, but the responses of the characters to the maternal effects may have differed qualitatively.

The hypothesis that the offspring of field females were influenced by distinct values of maternal effects could be tested if the proximal factors resulting in discontinuous values of maternal effects were identified. For example, if larvae initiating diapause in their second or third instar yield two "groups" of females, we would expect the two "groups" to produce offspring attaining unequal live larval and pupal weights, but showing similar development times and diapausing incidences. Parent-offspring regressions of live larval and pupal weight, measured using field parents sampled within a single "group", should also yield heritabilities that would be significant and similar to the estimates obtained using laboratory parents. Finally, this argument also suggests that the greater phenotypic variance observed in the first as compared to the second generation could at least in part have been due to the different values of the maternal effects associated with the insect "groups".

In this study, offspring were raised in isolation from their mothers in constant conditions for three successive generations. The assumption that changes in gene frequency were minimal between the generations is critical in allowing me to attribute the among-generation variations in phenotypic means, variances and heritability estimates to differences in maternal effects. The large population sizes

(reflected in the small inbreeding coefficients) suggest that the role of random fluctuation in allele frequency was minimal in producing these changes. Variations in mean phenotypes incompatible with the selection differentials, and the patterns of the among-generation changes in parent-offspring and full-sib heritability estimates, also suggest that maternal effects played a major role in influencing the insects' phenotypes.

It was assumed that most of the variation in maternal influence between field and laboratory females was due to a change in the environmentally-induced variance (V_{em} and $V_{gm \times em}$). This is obviously a simplification since the contribution of among-female genetic variation (V_{gm}) to the maternal effects may also have differed between environments. Contrary to other models (Janssen et al.,1988, Kirkpatrick and Lande, 1989), the environmentally-induced variance was also assumed to contribute independently of the mothers' phenotypes to the maternal effect. Contributions independent of the mothers' phenotypes are suggested by the equal influence of males and females to the phenotype of third generation offspring, and the changes in significance of the parent-offspring regressions when first and secong generation parental values were used as independent variables.

This study confirms some of the findings of Chapter 4. First, high estimates of heritability were obtained for all characters when the variation in maternal effects was

minimized. Second, evidence was found for the presence of a negative genetic correlation between diapausing propensity and larval live weight, and of a positive genetic correlation between diapausing propensity and development time. The maintenance of these genetic relationships across environments suggests that they may represent a stable genetic constraint that could prevent the joint evolution of fast development and high propensity to diapause in this species (Schneider et al., 1989). The impact of the negative genetic correlation between diapausing propensity and larval live weight on the joint evolution of these traits was observed in the laboratory generations: a significant positive phenotypic correlation in larval weight was induced in the parents crossed to produce the third generation, after only one generation of assortative mating conducted on the basis of the parental propensity to diapause.

Many genetic relationships between pairs of traits suggested by the data of Chapter 4 were not found in this study. This is likely due to the change in environment; raising insects on an artificial diet also resulted in changes in heritabilities and genotype x environment interactions in another generalist herbivore, the gypsy moth (Rossiter, 1987). The presence of maternal effects has consequences for the interpretation of the results of Chapter 4. First, the family components of variance derived using a full-sib design may have been overestimated.

Second, the across- and within-host genetic correlations could also have been biased by maternal effects. The impact of a maternal effect can vary with the environment in which the offspring develop (Gould, 1988). However, without such an interaction, variation in maternal effects influencing the full-sib groups would have contributed to making the across-host correlations more positive. Therefore, the corrected correlations in feeding performance across hosts (Chapter 4) may best reflect the magnitude of feeding trade-offs. Finally, the bimodal diapausing pattern observed in Chapter 4 may have resulted from maternal influences, provided that qualitative changes in the influence of the maternal effects occur when the insects are fed on a different diet (Gould, 1988).

CONCLUSION

Maternal effects often produce responses in the offspring which seem adaptive to cope with spatially and temporally heterogeneous environments (Mousseau and Dingle, 1991). In this study, the impact of maternal effects on the heritability of the traits suggested qualitative differences in the response of the characters to the maternal influences. It was proposed that the characters responded independently to the variations in maternal effects transmitted by field mothers. Accordingly, some traits displayed a unimodal phenotypic response and others displayed a multimodal response in reaction to maternal

influences. Further work is needed to identify the proximal conditions influencing maternal effects and to understand the relationship between maternal effects and offspring development in this species.

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Chapter 6:

GENETIC VARIATION IN HOST SELECTION BEHAVIOR: WITHIN- AND BETWEEN-POPULATION VARIATION IN LARVAL HOST ACCEPTANCE IN THE OBLIQUEBANDED LEAFROLLER

SUMMARY

The genetic basis of variation in larval host selection was investigated within and between populations of the obliquebanded leafroller from agricultural monocultures or native hosts. I asked whether populations of this generalist insect differ genetically in host-selection behavior, as indicated by the norms of reaction of host preference.

Parent-offspring regressions and a selection experiment revealed significant genetic variation in larval dispersal rates from apple and broad bean. Selection for a high or low acceptance of broad bean resulted in correlated changes in acceptance of wild rose, but had no statistically significant impact on acceptance of apple. Based on optimal foraging arguments, I predicted that a population exploiting a monoculture should evolve a high acceptance of the host cultivated in that monoculture. Assuming that this later change in host acceptance would not result in a general increase of acceptance of potential hosts, I also predicted that pairs of populations each exploiting a different monoculture should exhibit "crossing" norms of reaction of host preference, when tested on the hosts grown in the two

monocultures. The later prediction was not met in two comparisons of pairs of populations exploiting different monocultures. In the first comparison, two sympatric populations had similar host-selection behavior and in the second, two allopatric populations differed in host responses, but not as expected. The prediction that monoculture populations should evolve a high acceptance for the host grown in that monoculture was supported in a third comparison between two allopatric populations exploiting a monoculture and a mixed forest.

The comparisons do not allow me to infer the cause of the behavioral differences among the allopatric populations, nor to delineate the grain of the environment over which the changes in behavior occurred. Nonetheless, the results suggest that the evolution of a high acceptance of a locally abundant host (by adaptive or non-adaptive processes) resulted in a generalization of host-selection behavior in this insect.

INTRODUCTION

The mix of plant species available to herbivorous insects can vary in space and time due to heterogeneity in the environment, disturbance, colonization, or interspecific interactions (Thompson, 1985). Variation in distribution and relative suitability of host plants may lead to evolutionary divergence in host-selection behaviors of insect herbivores (Otte and Joern, 1977, Jaenike, 1978, Courtney, 1982, Futuyma, 1983, Ward, 1987). Indeed, empirical studies show that arthropod populations can differ genetically in their response to host plants (Singer, 1971, Phillips and Barnes, 1975, Rowell-Rahier, 1984, Futuyma et al., 1984, Schneider and Roush, 1986, Thomas et al., 1987, Prokopy et al., 1988) or prey (Tauber and Tauber, 1987, Hedrick and Riechert, 1989).

The potential of a population to undergo selective changes in host selection is determined by three factors. First, genetically-based variation in host-selection behaviors must be present. Second, the genetic variation in host response must translate into different patterns of host use and have consistent fitness consequences in the habitat under consideration (Singer et al., 1989, Jaenike, 1990). Finally, the evolution of habitat-specific norms of reaction in host response will be facilitated if migration is low between the populations using different environments (Futuyma and Peterson, 1985, Via and Lande, 1987, Mousseau and Roff, 1989).

If gene flow between habitats is minimal, the rate of evolutionary change in host-selection behavior, and the norms of reaction in host responses observed within a population at a given time, may be influenced by the relative abundance of locally available plant species and the genetic correlations among preferences for these hosts (Chapter 3; Arnold, 1981, Via and Lande, 1985, Via 1987, Singer et al., unpublished MS). For example, if a positive genetic correlation exists between the acceptance of a highly suitable and a toxic host, the toxic host may be used by the members of a population if it is rare, but both suitable and toxic hosts may be avoided if the unsuitable host is abundant (Levins and MacArthur, 1969, Futuyma, 1983). Therefore, the presence of genetic relationships among choice of different hosts may have important consequences for diet breadth in phytophagous insects.

Insect populations exploiting agricultural crops are subdivided into large patches of single hosts and constitute a good system to study the effect of host distribution on the evolution of host-selection behaviors (Via, 1984, 1990). If migration is low between patches, the evolution of a preference for and performance on a locally abundant host may be less constrained by genetic correlations in response to other hosts than if migration is high (Via, 1991). Therefore, negative correlations between the choice of a newly exploited host grown in a monoculture and the "ancestral" hosts may result in the evolution of a narrower

diet, whereas positive or null correlations may lead to greater potential polyphagy (Futuyma, 1983). Little is known about the impact of host shifts on the evolution of resource preference in herbivorous insects (Thomas et al., 1987).

This chapter investigates the consequences of local changes in host-selection behaviors on the potential norms of reaction in host choice expressed by a generalist insect, the obliquebanded leafroller (OBL). Newly hatched OBL larvae may disperse on silk threads and differ in their acceptance of host plant species (Chapter 3). In Lepidoptera, larval dispersal results mainly in intra-habitat movements. In two moth species in which dispersal distances were measured, most larvae dispersed less than 150 m in normal climatic conditions (Mitchell, 1979, Masson and McManus, 1981). In the OBL, fewer larvae were trapped outside than inside infested orchards, which suggests that larval dispersal also results in localized movements (Gillespie, 1982). If larval dispersal involves a high mortality risk, hatchlings may be selected to increase their acceptance of a locally abundant host within genetically isolated populations (Chapter 3). If such evolutionary change involves a modification of the rank order of host preference (e.g. Singer et al., 1989), the comparison of host-selection behaviors between pairs of populations each exploiting a different monoculture should reveal "crossing"

norms of reaction of host preference for the hosts grown in these monocultures .

This study addressed three questions: first, whether variation in acceptance by larvae of hosts of different species is genetically based; second, whether there are genetic correlations among responses for different hosts within OBL populations; and finally, whether genetically-based changes in host acceptance result in narrowing or broadening of the potential diet of this insect. This latter question was addressed by comparing larval responses to unusual or locally abundant hosts between three pairs of populations exploiting habitats differing in host texture (*sensu* Stanton, 1983).

MATERIALS AND METHODS

Host acceptance may be defined as a positive response to a host following encounter (Singer, 1986). In this chapter, a larva remaining on a host at the end of a specific bioassay is judged to have "accepted" that plant. On the contrary, a larva having left the host at the end of the bioassay is assumed to have "rejected" the host. Therefore, the proportion of larvae remaining on a host at the end of a bioassay was used to measure larval acceptance of that host within a family or population.

The bioassay that was developed to measure larval dispersal from different hosts (Chapter 3) was used to estimate the heritability of apple acceptance and to compare

larval host-selection behaviors among populations. The procedure consisted of transferring ten larvae to the leaf surface of each branch of the host plants tested. The branches were then placed under perforated plastic containers (diam 27.5 cm, height 30.5 cm). The containers were lined-up in front of fans which provided a slight but constant flow of air. The number of larvae remaining on the branches was counted after 60 min.

The same procedure was used to conduct a selection experiment of larval dispersal from broad beans (*Vicia faba*), a suitable host for the OBL. To facilitate the recovery of the larvae that had initiated dispersal, smaller containers were used (diam 21.5 cm, height 13.5 cm). The larvae remaining on the plants were counted after 30 min. The bioassays were conducted at a temperature of 23 - 25 ° C. Larval age has been shown to influence host acceptance in the OBL (Chapter 3). Larvae used in the present experiment were less than 2 h old and originated from each female's first egg mass.

Unless otherwise stated, all insects were raised on an artificial pinto bean diet (modified from Shorey and Hale, 1965) at 25 ° C under a 16L:8D photoperiod. Sib-matings were never allowed. The egg masses providing the larvae used in the selection experiment and in the comparison among pairs of allopatric populations were transferred in the black head stage to a temperature of 7.5 °C, a 16L:8D photoperiod and a relative humidity approaching 100 %. The

low temperature synchronized larval hatching with light onset and facilitated the control of larval age in the tests.

Heritability of apple acceptance. A parent-offspring regression technique appropriate for "all-or-none" traits (Roff, 1986) was used to estimate the heritability of apple acceptance in the hatchlings. The parental generation was derived from a colony that had been collected in an apple orchard and raised for six generations on artificial diet. A careful rearing procedure was adopted to minimize changes in gene frequency in the colony during that period (Chapter 3). Ten larvae were distributed on each of ten Red Delicious apple branches (*Malus domestica*) to estimate the proportion of larvae remaining on apple in the parental and offspring families. For each family, the heritability of the proportion of larvae remaining on apple was calculated using the pooled results of the ten replicates.

Within each parental family, thirty larvae that were not used in the bioassay were raised to adulthood. The adults were mated assortatively with respect to their familial acceptance of apple and the response of their hatchlings was measured. Heritability estimates calculated using single parental values were corrected for assortative mating (Falconer 1981; p. 164). The phenotypic correlation among parents that must be calculated to make the

corrections was obtained using parental values measured on the underlying continuous scale (see Roff, 1986, 1990).

Selection experiment and genetic correlations in larval host acceptance. To confirm the results of the parent-offspring estimates, a selection experiment was initiated to produce lines with low and high dispersal rates from broad bean plants. Hereafter, these two lines will be designated as "stayers" and "leavers", respectively. The apple orchard that yielded the insects used to estimate the heritability of apple acceptance was sampled a year later (1989) to establish a new colony. After five generations, bean acceptance was estimated in 24 families (the base population), by testing sixty hatchlings per family, equally distributed among six plants. The height of the bean plants was between 20 - 30 cm when prepared for the tests. They were cut and trimmed to bear only their third and fourth pairs of unfolded leaves and were inserted in florist vials before receiving the larvae. At the end of the bioassay, the tested larvae were classified as "stayers", if they were found on the plant or "leavers", if they were found crawling in the container. "Stayers" and "leavers" were raised to adulthood and mated assortatively to generate a line of "stayers" and a line of "leavers". The first episode of selection was done by crossing the adults originating from the 8 families that demonstrated the highest or lowest bean acceptance among the original 24 families. These crosses

generated 15 families of "stayers" and 22 families of "leavers". To produce a second generation of selected individuals, moths from 11 of the 15 families with the highest bean acceptance were crossed to produce 19 families of "stayers". Thirteen of the 22 families with the lowest bean acceptance were crossed to produce 23 families of "leavers". To produce a third generation of selected individuals, adults from families with the highest bean acceptance (6 out of 19) were crossed to produce the "stayers". Moths from families with the lowest bean acceptance (8 out of 23) were crossed to generate the "leavers".

Third generation "leavers" and "stayers" were tested on bean plants and on apple and wild rose branches (*Rosa* sp.) to investigate whether responses to different hosts were genetically independent in this population. The bioassay consisted of measuring host acceptance in a single family on the three hosts simultaneously, using three branches per host. Families of "stayers" and "leavers" were tested alternately. The bioassays were conducted using the largest containers and the number of larvae remaining on the hosts was counted after 60 min. Potted bean plants bearing second to fourth unfolded leaf pairs were utilized in these tests. Comparisons of host acceptance between "stayers" and "leavers" were done using t-tests. Each branch was considered as a replication unit.

Comparison between pairs of populations. Larval host responses were compared between pairs of populations. For each pair, 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 in Winfield, B.C. The populations were separated by less than one km. They were known to have been present in the apple and cherry orchards for at least ten and six generations, respectively (Chapter 2 and Edwards, pers. comm.).

In the second comparison, larval responses to apple and blueberry branches (*Vacinium corymbosum*) were compared between a population collected in a blueberry field in Pitt Meadows, B.C. and insects originating from an apple orchard in Oliver, B.C. The blueberry population was collected in the "site 2" studied by Gillespie (1982). Therefore, if no extinction had occurred, the population had been using blueberry for at least 20 generations prior to the test. No precise information could be obtained for the Oliver population. The populations were separated by 400 km. No apple orchards were present in the vicinity of the blueberry field, nor is blueberry grown in the valley in which the apple orchard was located.

The last comparison was between larvae originating from an apple orchard in Winfield, B.C. and a population

collected in a mixed forest near Apex Mountain, B. C., about 250 km away. The same apple orchard used in the apple-cherry comparison was sampled a year later (1990) to provide the Winfield population. Obliquebanded leafrollers had been present in the mixed forest for at least four generations prior to collection. The dominant species in the forest included trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), mountain alder (*Alnus tenuifolia*), wild rose (*Rosa* sp.), snowberry (*Shepherdia canadensis*) and red-osier dogwood (*Cornus stolonifera*). The larvae were only found on mockorange (*Philadelphus lewisii*) and red-osier dogwood. Apple and mockorange were chosen to compare the larval responses between the populations. No apple trees were grown in the area surrounding the mixed-forest and mockorange was not seen near the apple orchard in Winfield.

Field larvae in their last three instars were collected and transferred to artificial diet. The adults obtained were paired and their offspring reared to adulthood. These second generation moths were crossed to provide the hatchlings used to measure larval host responses in the populations. Nine and 7 mating pairs obtained from field collected insects provided the eggs to establish the blueberry and mixed forest colonies, respectively. A larger number of insects were collected in the apple or cherry orchards (over 95 mating pairs in each orchard). The low

population densities in the blueberry field and mixed forest made collection more difficult than in the orchards.

To synchronize larval emergence in the blueberry and apple populations for the tests, the blueberry population was reared at a lower temperature than the apple population (i.e. 18 - 20 ° C versus 25 ° C). In a bioassay, dispersal rates of hatchlings from a single family were simultaneously measured on two hosts, using at least four replicates (branches) per host. The bioassays were conducted on each population of a pair alternately. Freshly cut branches were used, except for mockorange and blueberry branches that were kept in water for a maximum of three and nine days respectively, under a 7.5 °C temperature and a 16L:8D photoperiod, before being used.

Host acceptance was compared between pairs of populations using two-way ANOVAs. Population and host were considered as fixed effects and the number of larvae remaining on each branch constituted the observations.

Measurements of larval head capsule size. In the gypsy moth, larval dispersal behavior is influenced by hatchling size (Chapter 3). To determine whether OBL larval host acceptance could be similarly influenced by hatchling size, hatchling head capsule widths were measured in six populations using a microscope micrometer eyepiece. Head capsule widths were very similar and measured 0.22, 0.23 or 0.24 mm. The distributions of head capsule sizes were

compared among populations and among families within each population using two-way log linear models (BMDP, 1990). The among-family comparisons were done within four populations in which ten larvae in each of nine families were measured.

RESULTS

Heritability of apple acceptance. Acceptance of apple was highly heritable (Table 6.1). The estimates calculated using male or female parental values were similar to the estimate obtained using mid-parental values. This suggests that maternal effects did not influence larval acceptance in this experiment (Falconer, 1981).

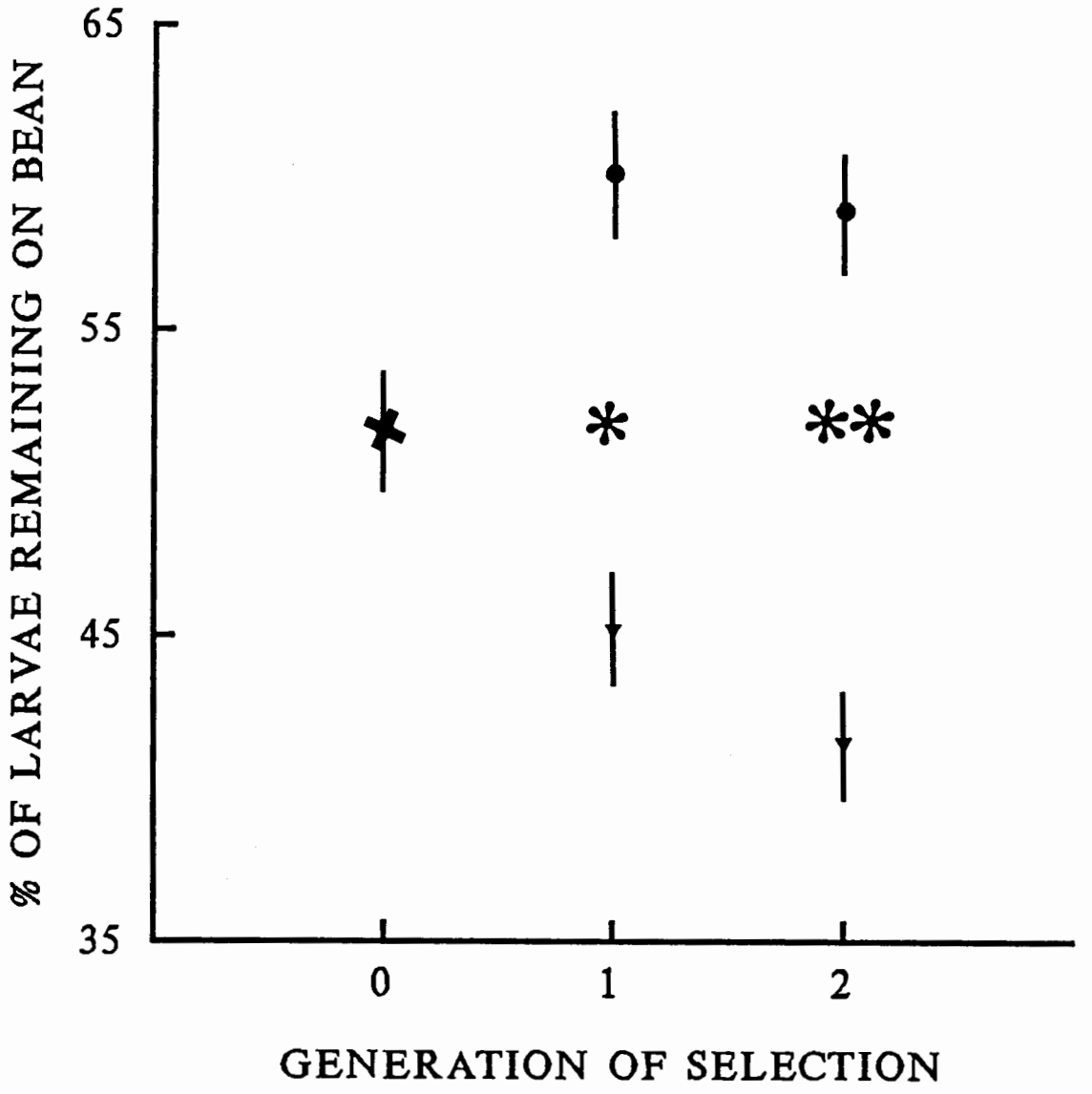
Selection experiment and genetic correlations in host acceptance behaviors. "Stayers" and "leavers" diverged in their acceptance of broad bean after only one generation of selection, showing that variation in larval responses to beans also had a strong genetic basis in that population (Figure 6.1). Acceptance of broad bean was greater in the "stayers" than in the "leavers" after three generations of selection (Table 6.2). The lines also diverged significantly in their acceptance of wild rose and tended to respond differently to apple, although this latter difference in behavior was not statistically significant (Table 6.2). The correlated responses to selection indicate

Table 6.1. Heritability estimates of OBL larval dispersal from the apple host

Regression	h^2 (± SE)
On Male Parent	0.76 (0.31)*[1]
On Female Parent	0.82 (0.26)**
On Mid-Parent	0.73 (0.17)**

[1] Significance of the regression coefficients:
*: P= 0.0047, **: P< 0.0003, df = 1,27

Figure 6.1. Percentage of larvae remaining on bean plants in the base population and after one or two generations of selection. Mean responses of the "stayers" and "leavers" are represented (± SE) by dots and triangles, respectively.



* t = - 6.131, P < 0.0001

** t = - 7.769, P < 0.0001

Table 6.2. Mean percentage of OBL larvae remaining on different hosts for lines selected to stay on (S) or leave (L) bean plants for three generations. The hosts presented to the larvae were bean (B), apple (A) and rose (R) branches.

Lines	Host	% remaining on hosts (± SE) [1]
S	B	74.9 (± 2.3)
		**
L	B	58.5 (± 2.3)
S	A	54.4 (± 3.3)
		N.S.
L	A	46.3 (± 2.9)
S	R	49.7 (± 2.8)
		*
L	R	41.9 (± 2.6)

[1] Proportion of larvae remaining on each host compared between "stayers" and "leavers" using a t-test. N.S.: P=0.072, *: P=0.046, **: P<0.0001

that a positive genetic correlation was present between acceptance of wild rose and broad bean in this population.

Comparison of pairs of populations. The lines joining the mean dispersal rate measured on different hosts within each population are just there to facilitate representation. There was no difference between the apple and cherry populations in their general acceptance of apple and cherry (Figure 6.2; Population effect, df = 1, 220, F = 0.03, P = 0.8574). The hosts were equally accepted by the larvae (Host effect, df = 1, 220, F = 3.33, P = 0.0693) and the populations showed similar responses to apple and cherry (Population x host effect, df = 1, 220, F = 0.50, P = 0.4801).

Larvae from the blueberry population had a greater general host acceptance than larvae from the apple population (Figure 6.3; Population effect, df = 1, 151, F = 26.46, P < 0.001). Apple was generally preferred over blueberry (Host effect, df = 1, 151, F = 46.61, P < 0.001), but the population x host interaction was not significant (df = 1, 151, F = 3.64, P = 0.2590). Consequently, insects from the blueberry field had higher blueberry and apple acceptances than insects from the apple orchard.

In the third comparison, insects from the apple orchard had a higher general host acceptance than insects from the mixed forest (Figure 6.4; Population effect, df = 1, 176, F = 11.01, P = 0.001). Apple was generally preferred over

mockorange (Host effect, df = 1, 176, F= 59.55, P < 0.001), but the norms of reaction of host acceptance were not parallel (Population x host effect, df = 1, 176, F = 64.80, P < 0.001). The two populations had similar acceptance of mockorange (Tukey tests, P > 0.05), but insects from the apple orchard had much higher acceptance of apple than insects from the mixed forest (Tukey tests, P < 0.05).

Measurement of larval head capsule size.

Comparisons among families. A small number of larvae per family was measured in the blueberry and apple population pair and the distributions of head capsule widths among families within these populations were not compared. The families within each of the other four populations did not differ in their distribution of head capsule sizes (all P's > 0.1312).

Comparisons among populations. The distribution of head capsule widths was similar among the mixed forest, blueberry and the two apple populations compared for larval acceptance (Population x size effect, df = 6, G = 5.49, P = 0.4826). The distribution of head capsule widths was also similar between the "stayers" and "leavers" (df = 2, G = 0.54, P = 0.7652). Thus, it appears that the variation in dispersal behaviors was not mediated by hatchling size.

Figure 6.2. Larval host responses in the sympatric populations collected in the apple (solid line) and cherry orchards (broken line).

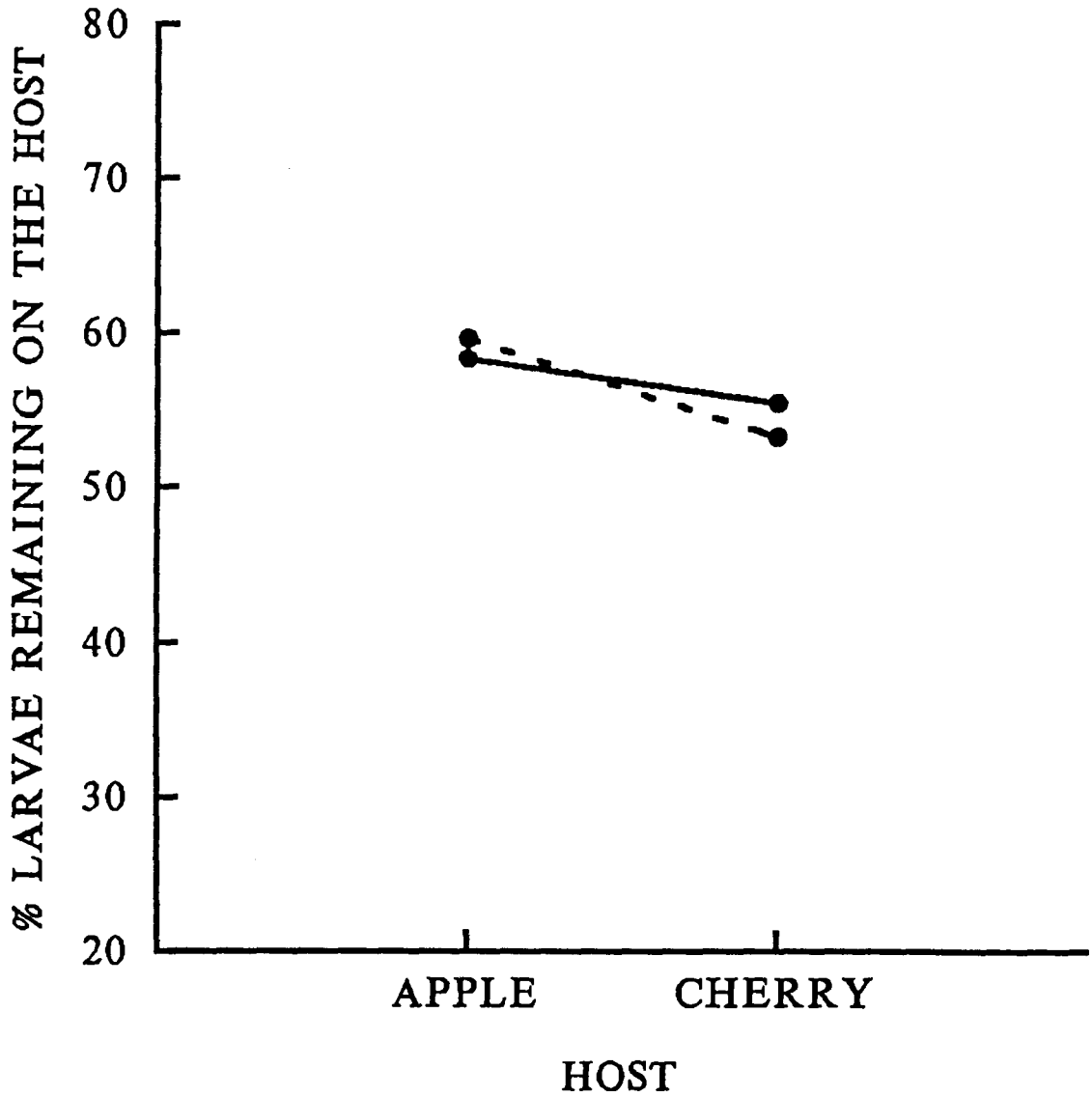

% LARVAE REMAINING ON THE HOST
80
70
60
50
40
30
20
APPLE
CHERRY
HOST

Figure 6.3. Larval host responses in the allopatric populations collected in the apple orchard (solid line) and blueberry field (broken line).

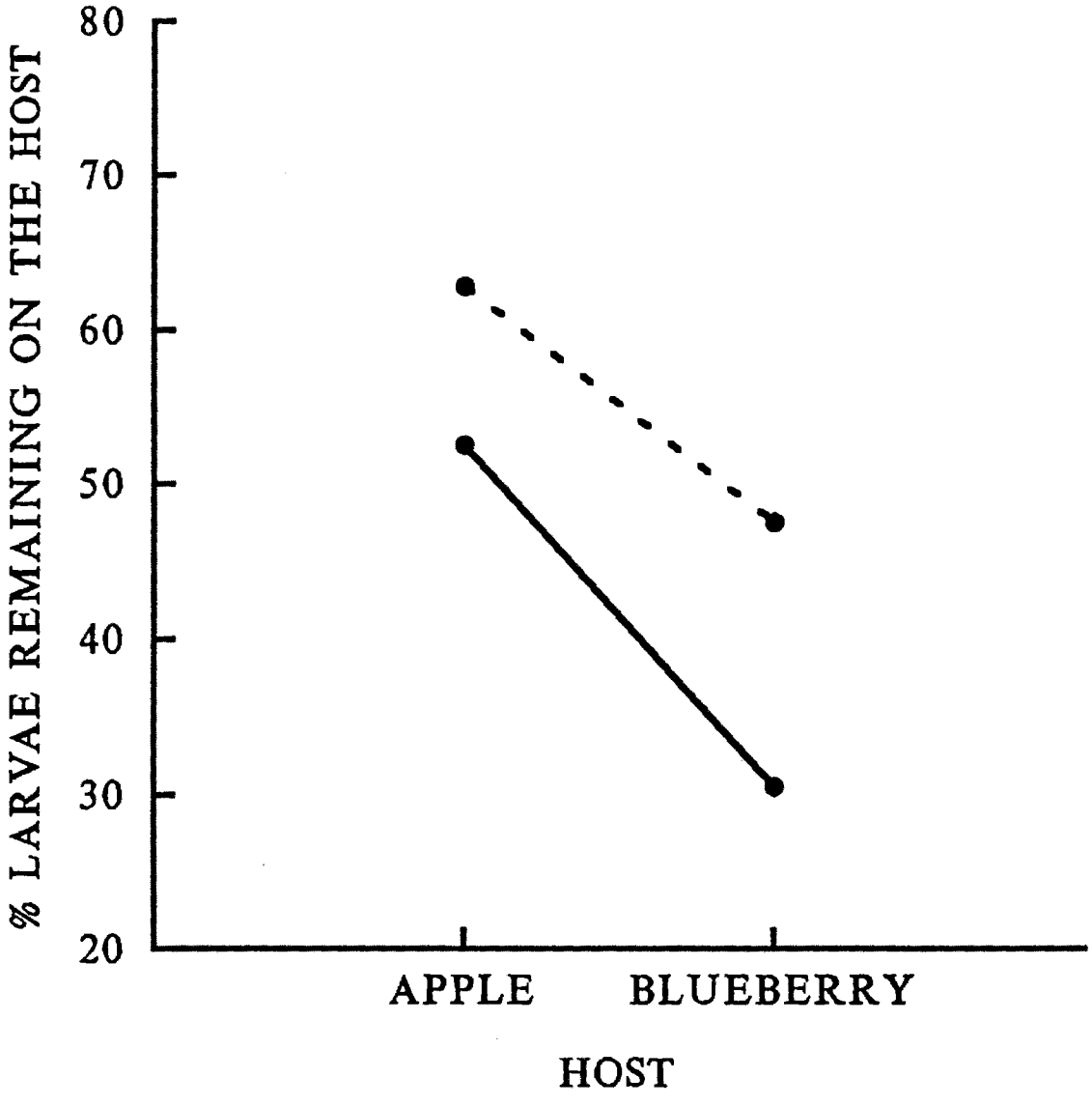
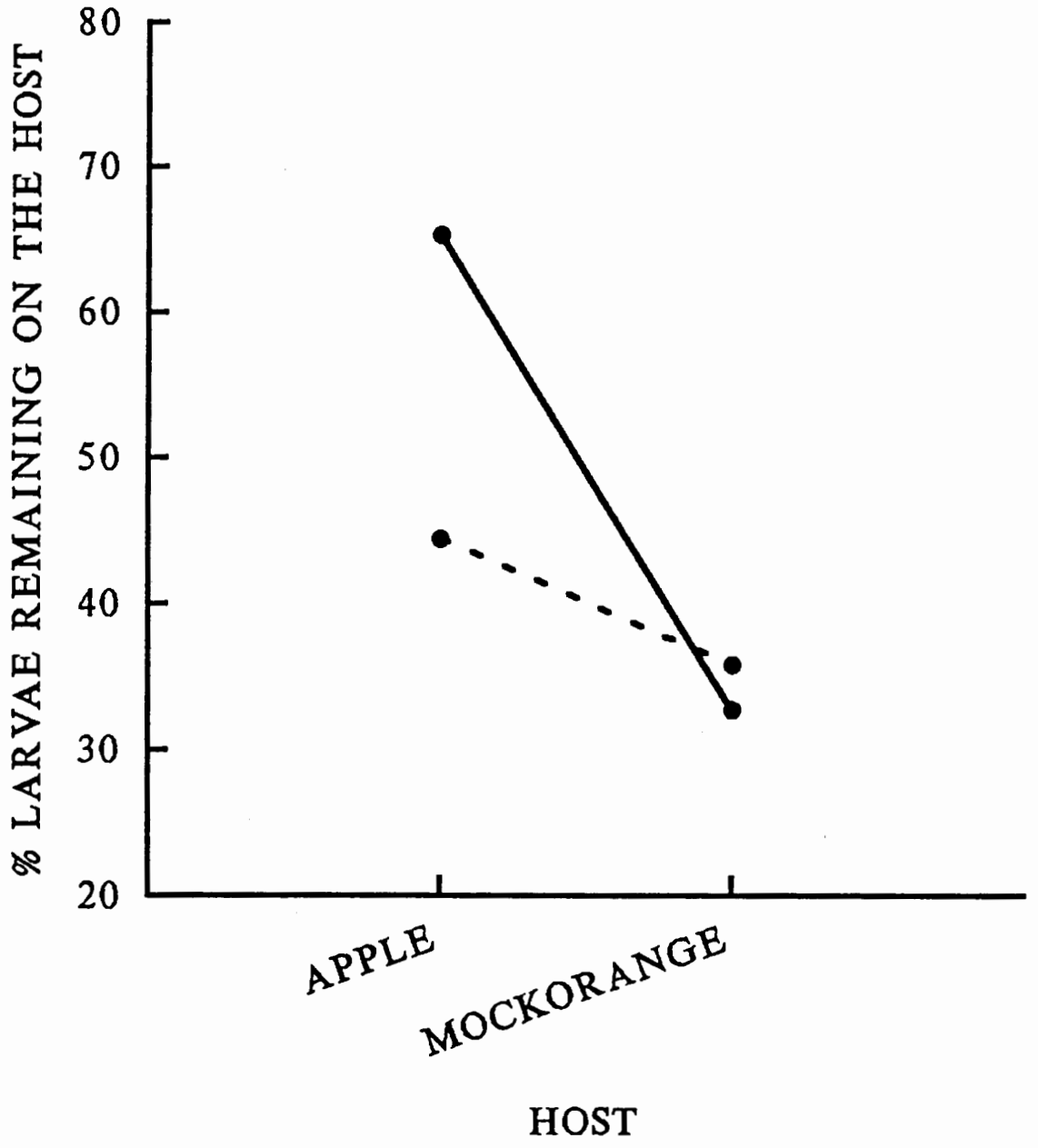

% LARVAE REMAINING ON THE HOST
80
70
60
50
40
30
20
APPLE
BLUEBERRY
HOST

Figure 6.4. Larval host responses in the allopatric populations collected in the apple orchard (solid line) and mixed forest (broken line).


% LARVAE REMAINING ON THE HOST
80
70
60
50
40
30
20
APPLE
MOCKORANGE
HOST

DISCUSSION

This study demonstrates that genetically-based variation in larval host acceptance was present within two populations of the obliquebanded leafroller. The selection experiment provides evidence that positive genetic correlations may exist between responses to different host plant species. The data also suggest that the norms of reaction in host response differed between the two pairs of allopatric populations but were similar between the two sympatric populations. However, the small number of parents used to establish the blueberry and mixed forest colonies may not be representative of the populations in these habitats. Therefore, more comparisons are needed to ascertain that populations differ genetically in their host responses.

Heritability of host acceptance. Genetically-based variation in oviposition preference is apparently common within populations of phytophagous insects (eg. Singer et al. 1988, Thompson, 1988a,b, Jaenike, 1989). Fewer investigations have reported genetically-determined differences in larval host-selection behaviors (Chapter 3). Selective changes in dispersal behaviors (host acceptance) were observed in a polyphagous mite confined to different hosts after less than ten generations (Fry, 1989). Genetically-based variation in food choice was also reported

in *Drosophila* larvae (Wallin, 1988). This is the first detailed study reporting within-population heritable variation in larval host acceptance.

Values of heritability always depend on the environment in which the measurements were completed and on the populations studied. However, the correlation between larval dispersal rates observed in the laboratory and the field (Chapter 3) and the independent estimates derived in two populations suggest that heritable variation in larval host responses is present in field populations.

Genetic correlation among responses to different hosts. Constraints on perception and/or discrimination among hosts may favor specialization in diet (Futuyma, 1983). When only one plant species is available locally, disruptive effects of selection modifying host perception could result in negative genetic correlations in responses to different hosts (Via, 1991) and thus favor diet specialization. Insect taxa that have been through major shifts in host use are often specialized behaviorally on the new host (Courtney and Kibota, 1990), which suggests that such disruptive effects could play a role in molding diet breadth in herbivorous insects. At present, there is no direct evidence for such a mechanism being the source of negative genetic correlations in host selection.

The "hierarchy-threshold" model (Singer, 1982, Courtney et al., 1989) proposes that many evolutionary changes in

host-selection behaviors may involve, at least initially, modification in insect specificity (*sensu* Singer, 1986) rather than in the rank order of host acceptability. One of the predictions of this model is that positive genetic correlations should be present between acceptance of low ranking hosts, a prediction that was supported in studies of specialist and generalist *Drosophila* species (Courtney et al., 1989, Courtney and Hard, 1990). A negative phenotypic correlation between discrimination within different "types" of an ancestral host and acceptance of a novel host was found in *Euphydryas editha* (Singer et al., unpublished MS). This relationship could also be due to among-population genetic variation in specificity. However, it was present in only one of the three *Eupydryas editha* populations that showed increased use of the novel host and therefore may represent a local rather than a general constraint influencing diet breadth in this species.

The significant parent-offspring regression in dispersal propensity from apple suggests that larval host selection can realistically be described as a threshold character in the obliquebanded leafroller. In such a model (see Falconer, 1981, Fig. 18.1), acceptance or rejection of a plant species is determined by the interaction of a normally distributed, genetically-based, underlying variable, and of a threshold. The underlying variable represents the motivational state of an individual to accept a host and the position of the threshold represents the

acceptability of the different plant species, as *perceived* by the insects within a particular population. Evolutionary changes in host selection may occur following a shift in the distribution of the underlying variable within a population (see Falconer, 1981, Fig. 18.1); this is equivalent to a change in the mean motivational state within a population. Evolutionary changes in host selection may also be caused by a change in the relative position of the thresholds; this corresponds to a change in host perception within a population.

A different proportion of the young larvae (< 2 h old) from a given family accepted each host species. This is equivalent to having all the thresholds (corresponding to the acceptability of the hosts) crossing the distribution of the underlying variable of the families. Accordingly, selection for a high or a low acceptance of broad bean, occuring through a change in the distribution of the underlying variable, is expected to produce a change in acceptance of the others hosts. However, if selection only influences the relative position of the thresholds, a change of acceptance of broad bean is possible without influencing larval response to other hosts. The selection for high or low acceptance of broad bean resulted in a correlated response to wild rose, and apparently modified acceptance of apple. The apparently higher correlated response to rose than apple may indicate selection that involved more than a modification in the general motivation of the larvae to

accept the hosts; selection may also have resulted in qualitative changes in host perception (i.e. in the way larvae perceive host stimuli and therefore rank their hosts).

The correlated responses to selection suggest that alleles influencing broad bean acceptance also modified acceptance of other hosts in the population studied. The sign of correlated selective responses and the nature of the genetic mechanism of adaptation may depend critically on the gene frequency that was present initially in the selected populations (Gould, 1988). Therefore, more experiments are needed to ascertain the generality of these genetic relationships in the obliquebanded leafroller.

Comparison of pairs of populations. Optimal foraging models suggest that the costs associated with discrimination (i.e., larval dispersal), may be balanced by the benefit of locating highly suitable resources. However, in populations segregated to monocultures, a reduction of searching costs may be the main factor influencing host acceptance, since the cultivated crop is virtually the only host present. This leads to the prediction that increases in host preference for the cultivated crop should be observed in populations remaining in association with monocultures for a sufficient time. Since this change in host-selection behaviors may occur through changes in the rank order of host preference or in specificity, pairs of populations

exploiting different monocultures are not necessarily expected to exhibit "crossing" norms of reaction of host preference.

In the blueberry population, larvae had a higher acceptance of blueberry and apple than in the apple population. Therefore, the patterns of host preference in the two populations do not support the hypothesis that populations expoiting different monocultures should evolve different rank order of host preference. This discrepancy may be due to two, non-exclusive factors. First, it is possible that a selective increase in blueberry acceptance occurred in the blueberry population and resulted in a correlated increase in apple acceptance (i.e. occured mainly through changes in specificity). Second, the between-population difference may have been caused by a low host acceptance in the Oliver population. Such a low preference of apple would be expected if the population had recently colonized the apple orchard. Indeed, acceptance of apple was relatively low in the Oliver population (52.1 %) compared to the other populations (Mixed forest; 44.4 %, Cherry orchard; 59.6 %, Apple orchards; 58.3 % and 65.3 %).

The comparison between the apple and mixed forest populations supports the hypothesis that an increase in host acceptance should occur in monoculture populations. Explaining the difference in response to mockorange between the mixed forest and apple populations is complex, but a higher acceptance of apple in the apple population was

expected. The high acceptance of apple by the apple population was not correlated with a high acceptance of mockorange. This indicates differences in host perception between the apple and mixed forest populations.

The comparisons of population pairs did not provide evidence that a higher preference for one host in a population resulted in a lower preference for another host in that same population (i.e. no "crossing" norms of reaction in host response were observed). This suggests that the evolution of a high acceptance of a locally abundant host favors polyphagy in this insect species.

The comparative method allowed for detection of among-population differences in host selection behavior but could not be used to *demonstrate* the cause of the changes in host acceptance (Endler, 1986). It seems reasonable to assume that the populations exploiting a monoculture shared the same loss of opportunity to locate a better host after dispersal from the cultivated host. Therefore, it is possible to infer that the changes in habitat host texture gave rise to the variation in larval host-selection behavior. However, the habitats exploited by the populations may also have differed in other ecological factors known to influence host-selection behaviors (Fox and Morrow, 1981, Thompson, 1988 c, Jaenike, 1990). For example, variation in habitat architecture influencing the mortality risk associated with larval dispersal may have favored local changes in host acceptance. Finally,

populational differences in host responses may also have been a consequence of genetic drift.

Adaptation in a spatial patchwork. Selective changes in the norms of reaction of host use among populations linked by gene flow can result from two processes: direct selection adapting each population to their local habitat and "general" selection influencing all populations in the patchwork (Via and Lande, 1985, Via, 1991). The contribution of these processes to influencing host use in a specific habitat is critically determined by the number and genotypic identity of the immigrating individuals.

The comparison between the adjacent apple and cherry populations indicates that no habitat-specific differentiation in larval host acceptance occurred. However, it is still possible that host responses evolved in these populations due to the effect of "general" selection. The allopatric populations diverged in host responses. At present, it is not possible to weigh the role of local or "general" selective processes, or of non-adaptive processes, in producing the divergences.

Insect populations may differ in genetically-based host-use traits. The grain of the habitat which delimits such variation differs considerably among insect species. It ranges from individual plants (Edmunds and Alstad, 1978, Karban, 1989), adjacent patches, fields or forest stands (Mitter et al., 1979, Schneider, 1980, Thompson, 1985,

Weber, 1986), to regions corresponding to allopatric sets of plant species (Scriber, 1988, Hagen, 1990). Obliquebanded leafroller females are reluctant to fly as indicated by the fact that some females appear to mate and lay their first egg mass very close to the host on which they pupated (Carrière, unpubl. data). Therefore, several generations may remain in the same habitat, which could promote adaptation to local conditions. More research is needed to determine the impact of environmental heterogeneity on divergence in host use characters in this species

CONCLUSION

A threshold model in which host preference results from the interaction of a genetically-based underlying variable, related to the motivation of an insect to accept hosts, and of thresholds representing the acceptability of host species, described well larval host-selection behaviors in the obliquebanded leafroller. A successful selection experiment which changed broad bean acceptance and resulted in a correlated change in preference for wild rose, and the comparison of the norms of reaction of host preference between pairs of populations from native and cultivated hosts, suggested that evolutionary changes in host preference may involve both a modification of the rank order of host preference and of specificity (the strength of host preference for a given physiological state). Whereas the cause of the change in the norms or reaction of host

preference among field populations is unknown, the data indicate that the evolution of a high acceptance for a locally abundant host resulted in greater polyphagy in the obliquebanded leafroller.

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Chapter 7:

CONCLUSIONS

These studies of the obliquebanded leafroller (OBL) evaluate the adaptation of larval feeding performance and host preference. Fox and Morrow (1981) proposed that insects that are generalists in food choice often function as local specialists. The significant heritabilities found in the feeding performance traits of OBL, and the presence of within- and among-population genetic variation in larval host-selection behavior, suggest that evolutionary change may lead to ecological specialization in generalist insects. These findings are important because few detailed studies have been conducted to investigate the evolution of host exploitation in generalist insects. In addition, my results support the hypothesis that specialization in host-selection behavior is driven by feeding trade-offs in phytophagous insects. To date, only two laboratory studies used a sufficiently high number of hosts to correct for potential influences of general vigor and/or maternal effects on the values of the genetic correlations in feeding performance on host-pairs (Futuyma and Philippi, 1987, Chapter 4). Both studies support the feeding trade-off hypothesis, contrary to several other experiments that did not consider such effects. Therefore, it is possible that the trade-off hypothesis has not been adequately tested to date (Jaenike, 1990). A number of studies suggest that genetic variation in host-selection behavior is common within insect

populations. However, there is at present little evidence to support the hypothesis that differences in patterns of host use among insect populations are due to genetically-based variation in insect host responses (Jaenike, 1990). This lack of evidence led Jaenike (1990) to propose that the genetically-based variation found in host responses within insect populations is neutral and nonadaptive. I have found that OBL populations may differ genetically in their host-selection behavior. These findings are in accord with the hypothesis that high searching costs favor the evolution of an increase in host acceptance within herbivorous insect populations, and therefore do not support the nonadaptive hypothesis mentioned above.

Apple leaves were more suitable than leaves from three alternative hosts commonly used by the OBL. Females produced by larvae that fed on apple leaves were heavier and more fecund than females fed on alternative hosts. Males trapped in the field and reared on the four host species in the laboratory did not differ in size (Chapter 4). Assuming that field moths originated from many host species, this suggests that the laboratory and field were similar environments with respect to larval growth, and therefore that apple was a highly suitable host for the population used to measure the fitness components. If it is assumed that the alternative hosts were representative of the host species available to the OBL in the Okanagan Valley, it could be concluded that the high suitability of apple leaves

is a factor that may favor the evolution of a high preference for that crop.

This conclusion is probably too simplistic, however. The significant relationship between fecundity and pupal weight indicates that pupal weight was under selection in the population used to estimate the host suitabilities. Moreover, pupal weight attained on apple was heritable (Chapter 4 and 5). This suggests that the high feeding performance observed on apple may have been the product of a recent evolutionary change. Comparisons of feeding performances of populations exploiting habitats with different host composition are needed to elucidate this point. Furthermore, the presence of trade-offs in feeding performance on apple and some of the alternative hosts complicates the predictions about the evolution of host range in the OBL. One effect of feeding trade-offs is that the evolution of a high feeding performance on apple reduces fitness on the alternative hosts. Therefore, a long term association with apple could select against migration leading to the exploitation of new hosts, and favor the evolution of a high preference for that crop (Chapter 4). Conversely, adaptation to the native hosts would reduce the benefit to the OBL of incorporating apple in its diet.

In the "classical" view, feeding trade-offs are believed to be a consequence of a differential allocation of fixed resources to the maintenance of competing detoxification mechanisms (Chapter 4). At genetic

equilibrium, alleles conferring either a high or a low ability to detoxify the hosts used by a population are expected to be fixed and absent, respectively. However, alleles influencing feeding performance positively on one host but negatively on another will have a smaller effect on fitness and will remain in high frequency for a greater period. This may result in "stable" feeding trade-offs within insect populations (Via, 1991). On the other hand, it was recently pointed out that the value of the genetic correlations in feeding performance could be influenced by selection (Stearns et. al, 1991, Via, 1991). If feeding trade-offs are easily modified by selection, it is more likely that their presence will be a consequence, rather than a cause, of the evolution of specialization in host selection behaviors (Futuyma and Philippi, 1987).

The stability of feeding trade-offs could be investigated in the OBL by comparing the values of the genetic correlations in feeding performance on host-pairs between populations exploiting a single host (i.e. monocultures) and populations using fine grained (*sensu* Levins, 1968) environments (i.e. mixed forests). These comparisons would also be useful to evaluate the evolutionary potential of the feeding performance traits.

Maternal effects often seem to produce responses in the offspring which are adaptive to cope with spatially and temporally heterogeneous environments (Mousseau and Dingle, 1991). While the role of maternal effects is unknown in the

OBL, it was found that they have the potential to affect offspring characters independently within the same organism (Chapter 5). This was demonstrated by the differential influence of maternal effects on the heritability of specific characters. A mixed larval strategy for larval diapause was found in the summer. This can be explained theoretically as a way of spreading the risk of reproductive failure in temporally unpredictable environments (Chapter 2). Experiments are needed to verify if larvae initiating diapause at different periods (summer or fall), or in their second or third instar, produce spring females which transmit "discrete" maternal effects to their offspring. Such "discrete" maternal effects could result in a multi-modal distribution of offspring phenotypes on each host. Therefore, in the absence of a maternal effect x host interaction, some families could have either high or low values for specific characters across all hosts, and maternal effects would have biased positively the estimates of the genetic correlations in feeding performance (Chapter 4). Maternal effects have not always been considered in the few experiments done to estimate feeding trade-offs in phytophagous insects (e.g. Rausher, 1984, Futuyma and Philippi, 1987). The findings of Chapter 5 suggest they should be seriously considered in the future.

Larval dispersal rates differed on four host species (Chapter 3). They were not influenced greatly by seasonal changes in the hosts, nor by differences in leaf age within

a host. Host-specific stimuli (the availability of refugia, leaf texture, and leaf odor) were apparently important in influencing larval host-selection behavior. In Chapter 6, it was demonstrated that part of the variation in larval host selection is genetically based within OBL populations. The between-population comparisons also revealed the presence of genetically-based differences in larval host preference. Although the differences in larval host responses were consistent with the hypothesis that high search costs favor the evolution of a broader host acceptance in herbivorous insects, more comparisons between populations exploiting different habitats are needed to confirm this hypothesis.

An important question that has to be addressed concerns the grain of the environment over which evolutionary divergence in life-history traits (Chapters 4 and 5) and host-selection behavior (Chapter 6) occur in the OBL. The diapausing trait (Chapters 2 and 4) may prove to be an excellent character for investigating the size of this grain, because it is relatively easy to measure (contrary to larval dispersal, for example) and has a genetic basis. The concordance of pesticide applications with specific events of the OBL life cycle differs in various fruit crops, because the "target" pests in each crop have different life histories, and the harvesting periods differ among the crops. A prediction can be made that OBL populations associated with crops regularly sprayed after the initiation

of the first flight (e.g. apple) should evolve a high incidence of larval diapause compared to populations exploiting crops left unattended after that period (e.g. cherry). Comparing populations using different crops in the same locality should therefore be informative on the potential for evolutionary divergence in the OBL. I conclude by suggesting that evolutionary changes in host selection behavior and life-history traits may be mechanisms by which the obliquebanded leafroller adopts a locally restricted diet breadth.

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