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The influences of host plant and genetic resistance to *Bacillus thuringiensis* on trade-offs between offspring number and growth rate in cabbage loopers, *Trichoplusia ni*

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Abstract. 1. Variation in progeny size and quality is common among insects and this variation can strongly influence individual fitness. Larger progeny typically survive better and develop faster under adverse conditions and may have higher fecundity. Due to resource limitations, however, trade-offs may arise between having fewer large offspring or more smaller ones.

2. For cabbage loopers, *Trichoplusia ni*, pepper leaves are a poorer larval host than cucumber or tomato leaves as indicated by survival, development rate, and body size. Moths reared on cucumber produced more slower growing offspring than those that had been reared on pepper, which produced fewer, faster growing progeny.

3. Traits conferring resistance to *Bacillus thuringiensis* (*Bt*) generally are associated with strong deleterious effects that may influence resource allocation and reproductive trade-offs between progeny size and number.

4. Unlike the host-plant related trade-off between progeny size and fecundity observed among susceptible control moths, *Bt*-resistant parents had both the lowest fecundity and smallest progeny size on all host plants. This finding suggests that the progeny size–number relationship is constrained in resistant individuals.

Key words. *Bacillus thuringiensis*, fecundity, fitness costs, maternal effects, resistance, parental effects, transgenerational plasticity.

Introduction

For herbivorous insects the quality of the parental host plant can extend to the next generation via transgenerational (i.e. parental or maternal) effects (Rossiter, 1996). For example, nutritional deficiencies can be transmitted from the parental generation to progeny such that the offspring of nutritionally deprived parents are less competitive than progeny of well-fed parents (Fox & Mousseau, 1998). Non-adaptive parental effects may impede the response of an insect population to its environment and ultimately affect the long-term persistence of the population (Rossiter, 1996).

Parental effects may, however, be beneficial and may improve the fitness of offspring in marginal habitats or stressful conditions. If the environmental experience of the parental generation is a reliable indicator of future conditions, then parents would experience higher fitness if they altered progeny size and number accordingly. *Daphnia* mothers reared under low food availability produce fewer larger offspring than mothers reared under better conditions (Gliwicz & Guisande, 1992). The large offspring were better able to tolerate periods of starvation than were smaller offspring. In the solitary bee, *Megachile apicalis*, offspring size and number vary with season such that fewer larger offspring are produced in the summer (Kim & Thorp, 2001). Similarly, female *Bicyclus anynana* butterflies

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at a low temperature produced fewer but larger eggs than females kept at a higher temperature (Fischer *et al.*, 2003). Thus, trade-offs between progeny size and number can respond to environmental conditions.

Another impact of environmental variation arises when stressors, such as disease or chemical toxins, select for resistance that is associated with fitness costs (Mcnair, 1991; Orr & Coyne, 1992; Carriere *et al.*, 1994). These fitness costs may influence the expression of the trade-off between fecundity and offspring size. Resistant individuals are thought to partition a greater proportion of resources to the maintenance of resistance traits, and this may thereby reduce the availability of resources for reproduction (Carriere *et al.*, 1994; Bergelson & Purrington, 1996). Constraints on the availability of resources may affect characters associated with reproduction, and thus could influence the size and number of offspring produced by resistant mothers.

The cabbage looper, *Trichoplusia ni*, is broadly polyphagous and feeds on over 160 host-plant species (Sutherland & Greene, 1984). It is also a major pest of cruciferous crops (Shelton *et al.*, 1982), is damaging to other field crops such as cotton and soybean (Jost & Pitre, 2002) and in British Columbia, Canada it is a pest of vegetable greenhouse crops (Janmaat & Myers, 2003). The ability of *T. ni* to use a wide variety of hosts both concurrently and in succession is key to its pervasiveness as a pest species. However, its performance varies considerably among different host plants. In host acceptance studies, *T. ni* exhibits high fecundity and rapid growth when grown on cruciferous crops, but has a longer development time and decreased fecundity on pepper (Sutherland, 1966).

The range of suitability of host plants for *T. ni* development suggests that transgenerational effects may be pervasive in this species. The performance of *T. ni* varies considerably among the three major vegetable crops grown in commercial greenhouses (cucumber, tomato, and pepper) (Janmaat & Myers, 2005). Surveys of progeny from parental *T. ni* populations grown on different host plants indicated a significant effect of parental host plant on progeny growth (preliminary observations). In addition, resistance to the microbial insecticide, *Bacillus thuringiensis* (*Bt*), has been recently detected in greenhouse populations of *T. ni* and is associated with significant fitness costs (Janmaat & Myers, 2003). Here, the effects of three different host plants on *T. ni* growth across four *T. ni* genotypic lines (resistant, susceptible, and two reciprocal hybrid crosses) and the effects of the parental host plant on progeny growth (indicated by their size after feeding for 7 days) are examined.

Methods

Trichoplusia ni larvae were reared on each of three host plants to examine effects on the growth of the parental generation and influences of the parental environment on progeny growth in a common environment. The effects were examined across four genotypes, which consisted of two parental strains (P_S and P_R) and their reciprocal hybrids (F_1f, F_1m).

History of Trichoplusia ni *colonies*

A *T. ni* colony, resistant to *Bt*, was initiated from 74 individuals collected from pepper plants in a commercial greenhouse in British Columbia, Canada in 2001 (labelled P5 in Janmaat & Myers, 2003). Two colonies were initiated in the laboratory from the collected field population on a wheatgerm-based diet (Ignoffo, 1963) and reared at 26 °C, L:D 16:8 h with uncontrolled humidity. One colony, the susceptible line (P_S), was reared without any exposure to *Bt* and exhibited a significant decrease in resistance after seven unselected generations in the laboratory (from 49.5 to 4.3 kIU ml^{-1} artificial diet) (Janmaat & Myers, 2003).

The other colony, the resistant line (P_R), was selected with *Bt kurstaki* (DiPel WP, Valent BioSciences Corporation, Libertyville, IL, U.S.A.) during each generation of laboratory culture to maintain resistance [P_R-UBC strain in Janmaat *et al.*, 2004)]. The resistant line (P_R) was exposed to *Bt*-mixed in artificial diet as groups of 20–25 5-day-old larvae (second and third instars) in 175-ml Styrofoam cups. All live larvae were transferred to cups with new artificial diet without *Bt* after 2 days. Surviving pupae were collected and pooled in a mating cage to produce progeny for the next generation.

Trichoplusia ni *crosses*

From the resistant and susceptible populations, four genotypic lines were produced. These genotypic lines were grown on each host plant to examine if the growth of parental and progeny generations varied across genotypes. Two generations prior to initiation of the experiment, individuals from the resistant colony (P_R) were reared on wheatgerm diet without the addition of *Bt* to reduce potential sub-lethal effects that may be passed on to offspring from parents. For three generations prior to the experiment, the P_S population had been reared on pepper leaves (see Methods below) and for nine earlier generations the P_S population had been reared on wheatgerm diet. In total, the P_S population had not been exposed to *Bt* for 12 generations.

Pupae from each population were sexed and mass crosses of 40 males and 40 females were initiated to produce four genotypic lines: resistant and susceptible (P_R and P_S respectively) and two reciprocal hybrids (F_1f: the resistant parent is the female and F_1m: the resistant parent is the male). Offspring of the mass crosses were assayed on *Bt*–wheatgerm diet mixtures to assess the resistance level of each genotypic line. All assays were performed with a minimum of four to six doses ranging from 2.5 to 80 kIU ml^{-1} diet and a control. Twenty-five larvae were assayed per dose for each bioassay. Larval mortality was observed 3 days following the experimental set-up (for additional discussion of methods see Janmaat & Myers, 2003).

The LC_{50} values (95% confidence interval or CI) of the different genotypes were 26.0 (16.9–39.9), 5.1 (3.4–7.6), 4.3 (2.9–6.3), and 3.5 (2.4–5.0) kIU ml^{-1} diet for the P_R, F_1f, F_1m, and P_S genotypes respectively. LC_{50} values and CI were estimated using the probit analysis procedure in Genstat 5 Release 4.1 (Rothamsted Experimental Station, 1998). Control mortality was < 5% for all genotypes and was not included in the probit analyses.

Host plants and Trichoplusia ni *growth measurements*

Each genotypic line was reared on three different host plants to produce the parental generation. The three different greenhouse crops (bell pepper: variety 444; beefsteak tomato: variety Rapsodie; and long-English cucumber: variety Ventura) were grown in a greenhouse (ambient light and temperature) at the University of British Columbia, Canada from August to October 2002. Plants were used ≈ 2 months after planting and before flowering. Neonates were placed onto leaf pieces (3 cm^2) contained in 60-ml plastic cups (five neonates per cup). The plastic cups were placed inside covered seedling flats lined with moistened paper towelling to maintain the turgidity of the leaf pieces. All leaf pieces were rinsed with a dilute hypochlorite solution (15 ml hypochlorite diluted in 4 litres of water) to remove pathogens and residues of a whitefly infestation.

After 3 days of feeding, surviving larvae were transferred to 175-ml Styrofoam cups. Larvae were kept in their original groups (five or less) until they reached the fourth instar. In the Styrofoam cups, leaf pieces were hung from wire hooks attached to lids of cups and the size of the leaf piece varied with larval size. The bottom of each cup was removed and the cup was inserted into a 30-ml plastic cup that could be replaced to allow for easy removal of frass. The Styrofoam cups were placed inside covered seedling flats lined with moistened paper towelling. New leaf pieces were provided every 2 days to early instars and daily to fifth instars in the Styrofoam cups. Fully expanded leaves located within the top third of each plant were chosen for feeding. Frass was removed when new leaf pieces were provided. Larvae were maintained at 26 °C with a L:D 16:8 h photoperiod.

Sixty neonates from each genotype were placed onto leaf pieces from each host-plant treatment group and reared until pupation. Pupae were weighed 2 days after pupation and sexed. Male and female moths were paired within their respective genotype and host-plant treatment group. Pairs were placed into 240-ml paper cups, kept at room temperature and supplied with 10% sugar solution. The cups were lined with black construction paper for oviposition and papers were changed every 3 days after adult emergence. Eggs were counted for each pair to estimate fecundity.

Eggs produced by each genotypic pair were hatched and 25 offspring per pair were each placed onto 1 ml of wheatgerm diet in a 30-ml plastic cup and kept at 26 °C. Offspring were weighed after 7 days of growth. Larvae from two to five pairs were weighed for each genotype–host-plant combination.

Statistical analyses

Survivorship of the parental generation was measured as the number of larvae surviving to pupation and was analysed using the nominal logistic procedure in JMP 5.0.1.2 (SAS Institute Inc., 2003) with genotype, host plant, and their interaction as factors. Pupal weights, fecundity, and offspring size were analysed using a general linear model (GLM) in JMP 5.0.1.2 with host plant and genotype, and their interaction defined as main effects. Sex was included as a factor in the pupal analysis, and the adult pair nested in host plant and genotype was included as a random factor in the analysis of offspring weight at 7 days. Rearing cup was included as a variable in the initial analyses and was not found to significantly affect the measured variables and therefore was removed from the final analyses. Offspring weight was analysed over all genotypes initially without a host-plant–genotype interaction factor due to the absence of offspring from the P_R–pepper treatment group. Offspring weight was then reanalysed, excluding the P_R genotype, to test for the presence of a host-plant–genotype interaction. Genotype and host-plant effects were compared using Student's *t*-test multiple comparisons on least square means produced from the full GLM assuming equal variances. Genotypic effects were further compared within each host-plant treatment group. Correlations between pupal weight, larval weight, and fecundity were analysed using Pearson product-moment correlations in JMPIN 4.0. Response variables were square-root transformed where appropriate to improve normality and homogeneity of variance and transformations are described in the results (Zar, 1996).

Results

The influences of the host plant on growth of both the parental generation and on the progeny weights were measured. First, the 'effects' of host plant on the parental generation followed by a description of the transgenerational effects of the parental host plant on the progeny generation reared on a common diet are reported. The effects of the parental host plant on both generations is further separated by resistance genotype.

Parental generation

Pupal weights of the parental generation differed significantly between host-plant treatment groups, demonstrating that the host plants differ in suitability for *T. ni* growth (Table 1). Pupae from the cucumber and tomato treatment groups were significantly larger than pupae from the pepper treatment group. The pupal weights were 187 ± 2 mg,

Table 1. Analysis of variance tables for pupal weight, fecundity, and offspring weight analyses. The effects of host plant and genotype on offspring weight were analysed both with and without the resistant P_R genotype due to the absence of the P_R–pepper treatment group. The response variable fecundity and offspring weight were square-root transformed in all analyses.

	d.f.	SS	*F*	*P*
Pupal weight				
Genotype	3, 205	0.001	0.78	0.50
Host plant	2, 205	0.050	57.07	<0.0001
Plant × Genotype	6, 205	0.007	2.73	0.014
Sex	1, 205	0.021	48.11	<0.0001
Fecundity				
Genotype	3, 33	436.2	5.81	0.003
Host Plant	2, 33	397.9	7.96	0.001
Plant × Genotype	6, 33	201.3	1.34	0.26
Offspring weight (with P_r)				
Genotype	3, 21	15.6	3.46	<0.03
Host plant	2, 21	13.4	4.45	<0.02
Pair (Genotype, Plant)	21, 708	143.1	4.54	<0.0001
Offspring weight (without P_R)				
Genotype	2, 18	0.27	0.08	0.92
Host Plant	2, 18	13.7	4.35	0.03
Plant × Genotype	4, 18	6.1	0.97	0.45
Pair (Genotype, Plant)	18, 599	112.3	3.96	<0.0001

180 ± 3 mg, and 152 ± 3 mg for the cucumber, tomato, and pepper treatment groups respectively (mean ± SE). Therefore, the pupal weight decreased by 20% from the best host plant (cucumber) to the worst host plant (pepper). Male pupae were significantly larger than female pupae (male: 183 ± 2 mg; female: 163 ± 2 mg).

Significantly more individuals survived to pupation on cucumber (53%) as compared with the other treatment groups; 22% and 25% for tomato and pepper respectively ($\chi^2_2 = 62.1$, $P < 0.001$). Genotype did not have an overall significant effect on survivorship ($\chi^2_3 = 4.1$, $P < 0.25$). Similarly, genotype did not have an effect on pupal weight; its effect varied, however, with host plant as demonstrated by a significant genotype by host-plant interaction (Table 1). The pupal size of the resistant P_R genotype (175 ± 4 mg) was smaller than the susceptible P_S (189 ± 5 mg) and the F_1m hybrid (196 ± 4 mg) genotypes when fed cucumber, whereas there were no significant differences between any genotypes on the other two host plants (mean ± SE) (genotype effect within cucumber: $F_{3,102} = 4.17$, $P = 0.008$; tomato: $F_{3,45} = 0.36$, $P = 0.78$; pepper: $F_{3,56} = 2.42$, $P = 0.08$). On cucumber, the pupal weight of the F_1f genotype (182 ± 3 mg) did not differ significantly from the P_R and P_S genotype, but was significantly smaller than the F_1m genotype.

There was a significant positive correlation between pupal weight of either sex and fecundity (female: $r = 0.55$, $P = 0.0001$; male: $r = 0.41$, $P = 0.007$). The negative effect of pepper on pupal size was reflected in the fecundity of the individual pairs (Fig. 1, Table 1). Pairs that developed on pepper leaves produced 30% fewer eggs than pairs fed cucumber leaves, and 21% fewer eggs than pairs fed tomato. In addition, the genotype also significantly influenced fecundity. The resistant P_R genotype produced 30% fewer eggs than the other genotypes (Fig. 2). This reduction in fecundity was observed despite the observation that pupal weights did not differ significantly with genotype on tomato and pepper. Only one P_R pair in the pepper treatment group produced viable offspring and this pair produced only 75 eggs. Therefore, resistance to *Bt* was associated with an extreme fitness cost in this population. With respect to fecundity, there was no interaction between genotype and host plant, in contrast to the interactions observed for pupal size (Table 1).

Progeny generation

The weight of offspring, after 7 days of growth on a common diet, varied significantly with the genotypes and host plants of their parents (Table 1). The largest offspring were produced by pairs that had developed on pepper leaves, the smallest were produced by pairs fed cucumber leaves, and offspring with intermediate growth were produced by pairs fed tomato leaves (Fig. 1). Therefore, the pepper treatment group, which was associated with the lowest parental fecundity, was also associated with the largest offspring size after 7 days of growth. Conversely, the cucumber treatment group was associated with the highest fecundity, and the smallest offspring after 7 days of growth.

The genotype of the parental generation also affected offspring growth (Table 1). The resistant P_R genotype produced the smallest offspring at 7 days relative to the other treatment groups (Fig. 2). The P_R offspring were 20% smaller than their susceptible counterparts at 7 days. The hybrid offspring appeared to experience no negative effects, as there were no significant differences in offspring size

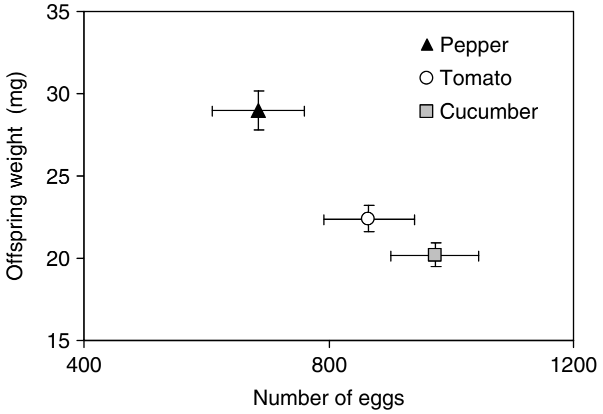

Fig. 1. Offspring weight at 7 days vs. number of eggs laid by *Trichoplusia ni* reared on pepper, tomato, or cucumber. Mean ± SE shown.

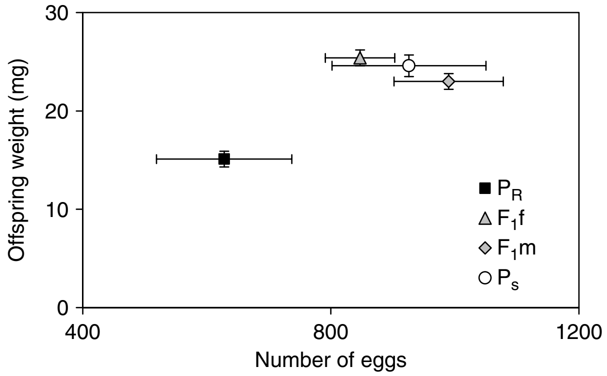

Fig. 2. Offspring weight at 7 days vs. number of eggs of different *Trichoplusia ni* genotypes. P_R, resistant; F_1f, hybrid with resistant mother; F_1m, hybrid with resistant father; P_S, susceptible. Mean ± SE shown.

between the hybrid and susceptible genotypes. The small offspring size of the P_R genotype was coupled with reduced fecundity of the mothers, which demonstrates the presence of severe resistance-associated fitness costs.

Discussion

Variation in the size of progeny both within and among insect populations is common, and this variation can have large effects on individual fitness (Fox & Mousseau, 1996). Progeny size and growth rates are often determined by egg size. Typically, progeny from larger eggs survive better, develop faster, and emerge as larger adults than progeny from smaller eggs (Fox & Mousseau, 1996). However, the advantages of larger egg size are not always demonstrated, and large size appears to be most beneficial in adverse environments (Fox & Mousseau, 1996). In the present study, the suitability of three host plants for *T. ni* larvae varied from the best host plant, cucumber, to the worst host plant, pepper. Tomato appeared to be a host plant of intermediate quality. Therefore, the difference in nutritional quality of these host-plants influences the life-history traits of the parental *T. ni* generation.

Females that experience poor conditions often exhibit reduced fecundity and produce progeny that are less vigorous due to the passive transmission of poor nutrition from parents to offspring (Rossiter, 1991). Therefore, under poor nutrient conditions it was expected that reduced fecundity would be correlated with reduced progeny size. Interestingly, in the present experiment, a negative relationship between fecundity and offspring size at 7 days was observed across the three host-plant treatment groups. Offspring of the most fecund cucumber treatment group were significantly smaller at 7 days than offspring of the least fecund pepper treatment group. Furthermore, both offspring size at 7 days and fecundity of pairs fed tomato leaves were intermediate to the other host-plant treatment groups. The results together suggest that there is a trade-off between egg number and offspring growth rate (Fig. 1).

In the present experiment, the development time to pupation and final pupal weight was not measured in the progeny generation and it is uncertain whether size at day 7 would influence progeny fitness. However, data from a similar study were re-analysed and showed that *T. ni* progeny size at 10 days was correlated negatively with time to pupation ($r = -0.73$, $P < 0.0001$) and correlated positively with pupal weight ($r = 0.29$, $P < 0.0001$) (data from Janmaat & Myers, 2005). Because pupal size was correlated positively with fecundity, as shown in the present study, and lengthened development times are predicted to increase the risk of predation or parasitism (Awmack & Leather, 2002), it is likely that the observed differences in progeny size would have fitness consequences. It is possible that these fitness consequences may be greater for offspring developing on pepper rather than cucumber leaves, as larger progeny size has been shown to be more advantageous in harsher habitats (Fox & Mousseau, 1996). The cause of the difference in offspring growth is unclear, because egg mass was not measured. Therefore, it is not known if faster growing larvae originated from larger eggs.

Mortality during the parental generation was particularly high on tomato and pepper plants (78% and 75% respectively), relative to cucumber (47%). Differential selection may have occurred such that only the most vigorous individuals survived to produce rapidly growing offspring on poorer host plants. If this effect were solely due to the differences in mortality observed between the host-plant treatment groups, then a similar effect on fecundity and offspring size would be expected for the tomato and pepper treatment groups. However, fecundity and offspring size of the tomato-reared group were comparable to that of parents reared on cucumber, which experienced significantly less mortality. The correspondence observed in the progeny generation for the cucumber and tomato treatment groups may be due to the similarity in parental pupal weights. In contrast, feeding with pepper leaves resulted in a reduction in pupal size in the parental generation, which was coupled with a reduction in fecundity. Small pupal size may trigger an increase in investment in offspring at expense of fecundity, thereby producing faster growing progeny in the pepper treatment group relative to the other groups. Therefore, it is possible that non-genetic, environmental effects on the parental generation influenced the growth of progeny; however, more research is needed to effectively rule out the effects of differential selection.

If non-genetic parental alter effects progeny size and growth rate to better suit the environmental conditions expected in the next generation, then non-genetic parental effects can be adaptive (Fox & Mousseau, 1998). For example, females are often at a selective advantage if they produce many small offspring in good environments and fewer larger offspring in poor environments. The performance of the seed beetle, *Stator limbatus*, on *Cercidium floridum*, a poor host plant, is enhanced if progeny hatch from large eggs, but offspring from small eggs are sufficient for development on better quality hosts (Fox & Mousseau, 1996). Similarly, eggs produced by *B. anynana* females at a low temperature produced larger hatchlings that had a higher probability of reaching maturity at the low temperature than smaller eggs produced at a higher temperature (Fischer *et al.*, 2003).

Altering progeny quality is only beneficial, however, if the parental generation is able to predict the environmental conditions of the progeny effectively. *Stator limbatus* females are able to adjust egg size even when they are switched to a new host. This suggests that the females can directly assess the oviposition substrate (Fox *et al.*, 1997b). In contrast, in the present study *T. ni* progeny size was a product primarily of the larval feeding experience of the parental generation, because all progeny were reared on artificial diet or on pepper and all *T. ni* pairs oviposited on the same substrate. In a recent study, *T. ni* adults that had fed on leaves with an oviposition deterrent were more likely to oviposit on leaves treated with the deterrent than inexperienced moths (Akhtar & Isman, 2003). Therefore, if the larval feeding substrate of the parental generation is predictive of the progeny environment, due to induction of parental preferences, then altering progeny size accordingly could be beneficial.

Genotype effects

Resistance to *Bt* was associated with a significant fitness cost as shown by the reduced fecundity of the resistant P_R genotype and the reduced pupal weight of the P_R genotype in the cucumber treatment group as compared with the other genotypes. The decrease in fecundity of the resistant genotype was coupled with a decrease in offspring growth. Therefore, the lower production of eggs was not associated with an increase in growth of progeny as observed with poor food plant quality. This may indicate greater constraints on the reproductive ability of the resistant P_R genotype. Similarly, *Bt*-resistant *P. xylostella* genotypes have reduced egg fertility (Groeters *et al.*, 1994) and this reduction may be a manifestation of constraints on egg provisioning. Allocation theory suggests that the presence of resistance traits diverts resources from reproduction (Bergelson & Purrington, 1996), which could ultimately affect egg provisioning and the expression of trade-offs between progeny growth potential and number.

Trichoplusia ni is a generalist herbivore, and its ability to use a wide variety of host plants effectively may depend on transgenerational plasticity, as appears to be true for the generalist seed beetle *S. limbatus* (Fox *et al.*, 1997a). For example, egg-size plasticity has been shown to play a role in the expansion of the host range of *S. limbatus* (Fox *et al.*, 1997a). Progeny of parents reared on the poor host, *C. floridum*, have increased survivorship on the exotic new host *Chlorolecuon ebano*, thereby allowing *S. limbatus* to expand its host range. In heterogeneous environments where poor quality hosts cannot be avoided, selection for transgenerational plasticity is expected (Fox & Mousseau, 1996). Genotypes that have limited plasticity will be at a disadvantage in these variable environments. The success of *Bt* resistant genotypes will depend not only on the direct fitness costs associated with resistance but also on the availability of suitable host plants, and on the ability of the different genotypes to adjust to different host plants when necessary.

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