Arthropod-Plant Interactions (2013) 7:109–118
DOI 10.1007/s11829-012-9225-0

ORIGINAL PAPER

Effects of host plant and maternal feeding experience on population vital rates of a specialized leaf beetle

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Received: 13 January 2012 / Accepted: 6 September 2012 / Published online: 27 September 2012

Abstract In herbivorous insects, the interaction between adult preference and progeny performance on specific host plants is modified by maternal feeding experience and host plant quality. Ultimately, changes in the strength of this interaction can affect insect population dynamics. In this study, we hypothesized that adult host plant preference influences progeny performance through a maternal feeding experience × host plant interaction, that is, the effect of adult feeding experience on progeny performance will depend on the host plant. Second, that decoupling of the preference–performance relationship due to host switching results in different population vital rates changing population dynamics. An increase in development time and a decrease in body size of individuals in the alternate host should decrease population growth. We tested these hypotheses using two lines of the tortoise beetle *Chelymorpha varians* Blanchard fed with two hosts (*Convolvulus arvensis* and *Calystegia sepium*). Maternal feeding experience treatments were crossed with host plant species, and the offspring's developing time and adult size were measured. The host plant influence on the beetle's population vital rates was tested using stage-structured matrix population models and life table response experiments. Host plant preference affected offspring body size through a host plant effect that contributed to adaptive life history responses only in the better quality host. *C. varians*' population growth was positive when fed with either host; comparatively, however, *C. sepium* had a negative effect on growth by reducing all transition probabilities of the life cycle stages of the beetle. Here, we show that individuals of *C. varians* prefer and perform differently on distinct hosts and that these patterns influence population vital rates in different ways. When beetles prefer the host plant where their progeny performs best, life history responses and life stage transitions lead to higher population growth; otherwise, growth rate decreases.

Keywords *Chelymorpha varians* · Plant host preference · Life history performance · Population dynamics

Introduction

In phytophagous insects, the interaction between adult preference for and progeny performance on specific plant hosts can significantly influence the phenotype and life history of individuals (Rossiter 1996; Bernardo 1996; Mousseau and Fox 1998; Agrawal 2002). If adults mate, prefer to oviposit, and/or spend more time feeding on the host plant where their progeny performs best, then a preference–performance linkage will result in adaptive life history responses (Jaenike 1978; Mousseau and Fox 1998), which may translate into low amplitude and stable

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Handling editor: Joseph Dickens.

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population dynamics (Price et al. 1990; Price 1994). Conversely, if adult host preference is not coupled with progeny performance, life history responses can favor a generalized use of plant resources by larvae, probably leading to erratic population dynamics (Price 1994).

Although there is ample evidence for a link between preference and performance in insects across generations (e.g., Rausher and Papaj 1983; Thompson 1988; Mayhew 1997; Gratton and Walter 1998; Hue et al. 2007; Gripenberg et al. 2010), there are also several examples that show no correlation (e.g., Via 1991; Cronin and Abrahamson 2001; Mayhew 1997; Scheirs et al. 2000; Karban and Agrawal 2002). Adult insects can choose oviposition sites that enhance their own long-term fitness at the expense of their individual offspring (Scheirs et al. 2000). Understanding this variation in preference–performance relationships is a key to make predictions about life history responses and their influence on population dynamics (Gonzáles and Gianoli 2003).

Populations of the same species developing in different environments can differ in several demographic parameters, which can lead to differences in population growth rates (Caswell 1983). Specifically, for phytophagous insects, host plant quality can affect fecundity, survivorship and development rates (Larsson et al. 2000; Awmack and Leather 2002); thus, the reproductive output varies with the host plant where insects develop. Reproductive output can also be influenced by the mother's previous environmental experience. Maternal effects tend to increase the acceptability and preference of the original environment (Bernays and Weiss 1996; Fox et al. 1995; Fox and Mousseau 1998), facilitating host fidelity (Marshall and Uller 2007; Uller 2008; Agrawal 2002) and promoting adaptation (Mousseau and Fox 1998).

When a specialized insect herbivore switches to a host plant different than that of the maternal generation, the preference–performance relationship can alter life history performance traits. For example, a highly attractive plant can represent an extremely poor resource, a switch to it resulting in increased development time, reduced adult size and low offspring survival (Karowe 1990; Keeler et al. 2006; Casagrande and Dacey 2007; Keeler and Chew 2008). Likewise, a specialized herbivore exposed to a different host plant species suitable for development may fail to recognize it as an adequate food resource or oviposition site (Verhoeven et al. 2009). If changes in life history performance traits brought about by the use of an alternate host plant modify herbivore vital rates, populations may experience negative growth, local extinction (Birch 1948; Caswell 1983) and/or even eruptive outbreaks (Price 1994).

Although it has often been assumed that host plant effects on insect performance can translate into effects on insect population dynamics, empirical evidence is still scarce (Larsson et al. 2000; García-Robledo and Horvitz 2011). We have just begun to address the interplay between variation in life history performance traits and demography in original and alternate environments (e.g., García-Robledo and Horvitz 2011). The present study is a first step toward understanding how different preference–performance relationships, which occur when populations are subject to different environments, can alter population dynamics (but see Rossiter 1991). We consider the maternal previous feeding experience and host plant-mediated variation in preference–performance relationships of a specialized herbivore, and their consequences on insect population vital rates indicative of population dynamics. Assessing changes in life history responses, population growth and life stage transitions associated with decoupling of the preference–performance relationship as a consequence of host switches can help us understand future colonization success, range expansion and evolutionary responses of life history performance traits in specialized insect herbivores.

Preference and performance of the tortoise beetle *Chelymorpha varians* Blanchard (Coleoptera: Chrysomelidae: Cassidinae), whose larvae and adults feed exclusively on Convolvulaceae hosts (Artigas 1973; 1994), are addressed using individuals reared on two host plants, *Convolvulus arvensis* and *Calystegia sepium* (Convolvulaceae). Specifically, we tested two hypotheses. First, whether host plant preference by adults influences progeny performance through a maternal feeding experience × host plant interaction. Adults from the maternal generation should show preference for the host experienced by their parents, translating this choice into favorable life history performance trait values (e.g., fast development time and large body size). Second, we tested whether changes in the preference–performance relationship due to host switching result in different vital rates (i.e., population growth rate, λ, and life stage transitions). Decoupling of the preference–performance relationship should slow development time and decrease body size of individuals in the alternate host and, consequently, decrease population growth.

Materials and methods

Study species

The tortoise beetle *C. varians* Blanchard (Coleoptera: Chrysomelidae: Cassidinae) is a leaf-eating herbivore with a highly specialized diet. Both adult and larval stages feed exclusively on members of the Convolvulaceae family ("morning glory"). This beetle has been reported to feed on species of *Convolvulus, Calystegia* and *Ipomoea* (Buzzi 1988; Windsor et al. 1992; Artigas 1973; 1994; Costa et al. 2007).

Females oviposit egg clusters on the underside of leaves, and emerging larvae remain gregarious throughout their entire life cycle (Artigas 1973, 1994; Costa et al. 2007). The complete life cycle can take, on average, ca. 32 days (Hamity and Neder de Román 2008). Larvae are exposed to predators and parasitoids on leaf surfaces (Olivares-Donoso et al. 2000) and thus form a shield as a defense mechanism by storing feces and exuviate on moveable abdominal spines (Nogueira-de-Sá and Trigo 2005).

In Chile, *C. varians* beetles are found between 29° and 39° S and from 0 to 1,000 m (Borowiec and Swietojanska 2006; Zuleta et al. 2008). They feed on two perennial exotic vines native to Eurasia, *C. arvensis* L. and *C. sepium* L. (Pfirter et al. 1997). Both species are considered noxious weeds in Chile and numerous countries worldwide (Matthei 1995; Boldt et al. 1998). Whereas *C. arvensis* is abundant and widespread along open habitats between 19° and 44° S, *C. sepium* grows in shaded and moist habitats and has a narrower distribution range between 33° and 45° S (Matthei 1995).

Experimental design

Beetle rearing scheme

We created two maternal host lines of *C. varians* using adult beetles collected from both *C. arvensis* and *C. sepium* plants at the campus of Universidad de Concepción in Chile (36°49′39″S; 73°2′20″W). Although, beetle abundance was not specifically quantified, individuals were conspicuous and plentiful in both plant species. Likewise, both plant species were conspicuous in the area, although *C. arvensis* was easier to come across. Adults beetles were brought to the laboratory and kept in plastic cages to mate and produce clusters of offspring. Clusters were used to generate an F1 generation within each of the two maternal host lines, *C. arvensis* or *C. sepium*, and were fed with the host plant that their mothers experienced. Freshly collected leaves of *C. arvensis* or *C. sepium* were provided every other day. We reared ten F1 generation families in the *C. arvensis* maternal line and nine in the *C. sepium* maternal line. The F1 was used to perform host plant preference trials. Individuals were kept in Petri dishes under the same diet and mated to form an F2 generation used for the performance experiment.

Host plant preference

Using adult individuals (maternal generation) from an F1 generation, we conducted feeding choice trials on a 40 cm × 40 cm arena that contained a plant on every corner (two plants per species placed in alternate corners). Plants were of approximately the same size and in an infertile stage. Plants were placed in small pots and watered before trials began. From each of the two origins (*C. arvensis* and *C. sepium*), we randomly chose 10 males and 10 females representing all families. Each individual chosen was placed at the center of the arena and observed for a 10-min period. For each individual, we recorded the time spent feeding on *C. arvensis,* as well as on *C. sepium*. We ran trials one beetle at the time within a two-week interval. We obtained 20 independent trials per host plant.

Beetle performance

Using egg clusters from the F2 generation (see "Beetle rearing scheme"), we reared 15 families per maternal host line to establish experimental host plant treatments. From each egg cluster, half of the emerging larvae were assigned to a *C. arvensis* leaf feeding regime and the other half to a *C. sepium* feeding regime. Thus, the maternal host line treatment (maternal feeding experience effect) was crossed with the host plant treatment (host plant effect). Larvae were raised under treatment combinations with their respective family members until adulthood. Beetles raised under different treatment combinations were monitored daily throughout their lifetime recording, for each individual: (1) adult weight and (2) larval development time (from egg hatch to adulthood). These variables were used as a proxy of individual lifetime performance over treatment combinations.

Data collection and analysis

To evaluate host plant preference, we transformed, for each trial, the time spent feeding on each host species into a binary variable (choice of either *C. arvensis* or *C. sepium*). This was possible given that all beetles evaluated remained the entire time they spent on a plant, feeding on the host species they initially chose during the trial. Therefore, we know that beetles chose either one plant or the other in each trial. There was no evidence of erratic or switching preference behavior between plant species. Subsequently, we used a logit model with host choice as a dependent variable and maternal feeding experience as main effect. These and all subsequent analyses were conducted using the R statistical environment (ver. 2.12.1, R Development Core Team 2011).

To quantify the performance of *C. varians*, we considered the maternal feeding experience, host plant species and F2 families (random factor) nested within the maternal feeding experience treatment, as main factors. Development time and adult weight were used as dependent variables. Data were analyzed separately for each trait using an analysis of variance for a nested design (nANOVA). In both models, we calculated interaction effects between maternal feeding experience and host plant species.

A significant interaction indicates potential genetic differences between maternal lines in their capacity to switch host plants successfully. Significant differences among F2 families indicate genetic variation in life history performance traits within maternal lines. To assess the evolutionary potential of life history performance traits, we estimated genetic variation in development time and adult weight in relation to experimental treatments. For treatments that showed significant differences, evidence of a relationship between life history performance traits was evaluated by fitting general linear models (*glm* function in R) with a Gaussian error and an identity-link function. We used development time as an independent variable and weight as a dependent variable in the models. Replicates were based on mean F2 family values in all cases.

Effects of host plant on population growth of C. varians

To evaluate the effects of host plant on asymptotic population growth rate (λ), we estimated fecundity, development and survival in laboratory conditions by following the fate of all F1 *C. varians* individuals within each of the maternal host line treatments (*C. arvensis* or *C. sepium*). The life cycle of *C. varians* beetles is described by four discrete stages: eggs, larva, pupa and adults. Larval instars were not considered given that it was not possible to identify and follow them accurately. We only compared growth rates and changes in λ between host plants because previous maternal experience did not show a direct effect on adult size, a fitness correlate (see "Results"). Within each generation, individuals in a stage class survive, enter the following stage, or die. There is no retrogression, nor stasis (survival without transitioning), and only adult females contribute to the following generation. For each maternal line, we constructed a stage-structured matrix population model given by: $n_{t+1} = An_t$, where n_t and n_{t+1} correspond to the number of individuals in stage i at time t and time $t + 1$, respectively, and A is a transition matrix (Caswell 1996, 2001). Adult fecundity (F) was calculated as the average number of eggs oviposited per clutch per female. To calculate, for each host plant, the 95 % confidence interval of λ, we generated 1,000 bootstrap projection matrices by resampling from the set of observed transitions (Caswell 2001).

To identify the sources of differences in λ (i.e., life stage transitions) between populations, we used a life table response experiment (LTRE) (Caswell 2001). This analysis partitions the difference in λ into variation associated with matrix elements (Caswell 2000). Using this approach, we can assess how the host plant impacts λ and identify those vital rates (transition probabilities) that most contribute to differences in λ. All demographic analyses were carried out using the *popbio* package (Stubben and Milligan 2007) in R.

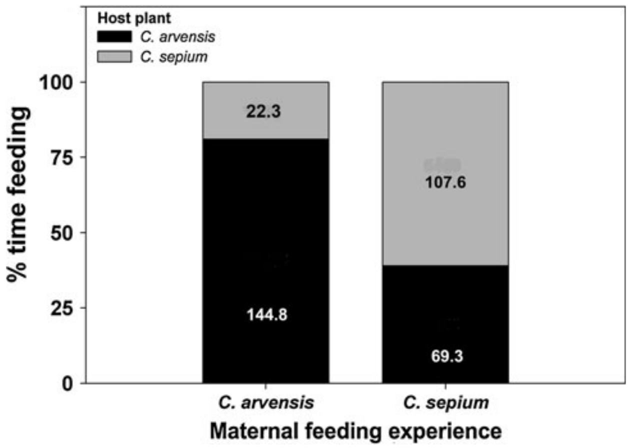


Fig. 1 Host plant preference of the F1 *C. varians* generation given by the percent feeding time invested by adult beetles from both host lines. Adults were subject to a test choice experiment. Numbers represent the total number of minutes that beetles spent feeding on each treatment combination

Results

Host plant preference

When preference was evaluated, the logit model revealed significant differences in host choice between maternal feeding experience treatments (estimate $= -1.50$, $z = -2.18$, $P = 0.0291$). Beetles chose to feed on the host plant of their parents but the strength of this choice varies with host plant (Fig. 1). Beetles that come from parents reared on *C. arvensis* chose *C. arvensis* 2.3 times more than *C. sepium,* whereas beetles from a *C. sepium* maternal host line chose *C. sepium* 1.5 times more than *C. arvensis*.

Beetle performance

Adults feeding on different host plants varied significantly in weight ($F_{1,23} = 34.95$, $P < 0.0001$). Individuals reared in *C. arvensis* were 20 % heavier than individuals reared on *C. sepium* (Fig. 2a). There were, however, no differences in weight between maternal feeding experience treatments (marginal effect: $F_{1,23} = 3.44$, $P = 0.0641$) and no significant interaction between maternal feeding experience and host plant treatments ($F_{1,23} = 0.0004$, $P = 0.9844$; Fig. 2a).

Individuals fed with *C. arvensis* took longer to reach adulthood than individuals fed with *C. sepium* ($F_{1,20} = 25.06$, $P < 0.0001$; Fig. 2b). Moreover, beetles that came from a *C. arvensis* maternal feeding experience also took longer to reach adulthood ($F_{1,20} = 24.37$, $P < 0.0001$; Fig. 2b). Development time, however, varied depending on the treatment combination. There was a significant maternal feeding experience × host plant interaction ($F_{1,20} = 4.83$, $P = 0.0286$; Fig. 2b). Thus, the decrease in

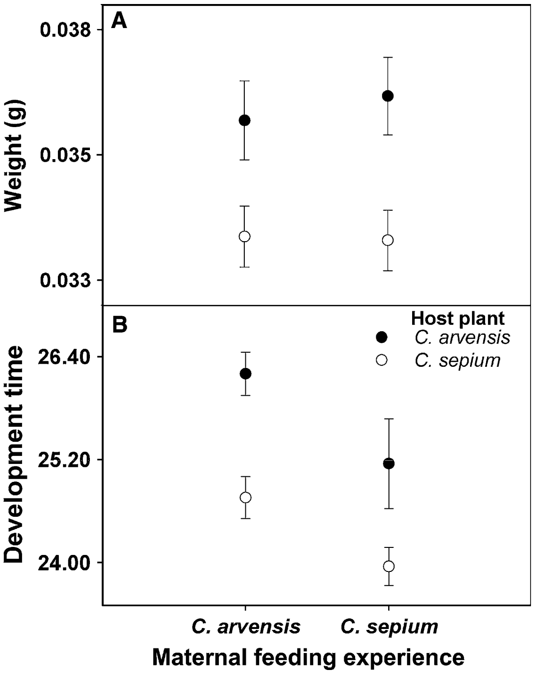


Fig. 2 Mean performance trait values (±SE) under different maternal host plant experience and feeding host treatments levels measured in the F2 generation. **a** Mean adult weight and **b** development time from egg to adult

development rate associated with feeding on *C. arvensis* was intensified when the maternal feeding experience was also *C. arvensis* (Fig. 2b).

There was significant variation among families nested within maternal feeding experience in weight ($F_{20,23} = 9.78$, $P < 0.0001$) and development time ($F_{17,20} = 29.23$, $P < 0.0001$). Thus, genetic variation in life history performance traits was detected within maternal lines (Fig. 3a–d). Families that came from a *C. arvensis* maternal host line ranged on average from 27 to 41 mg in weight ($s^2 = 0.0049$) and took from 23.1 to 30.3 days ($s^2 = 6.8121$) to reach adulthood. Families that came from a *C. sepium* maternal host line ranged on average from 16 to 45 mg in weight ($s^2 = 0.058$) and took from 15.1 to 28.9 days ($s^2 = 15.2881$) to reach adulthood. A significant relationship between life history performance traits was found within the *C. sepium* maternal feeding experience treatment; as development time took longer, individuals had on average lower average weight (Table 1; Fig. 4).

Plant host effects on population growth of *C. varians*

The average per capita fecundity F was 25 % higher for females from the *C. arvensis* line $\left(\bar{X}_{\text{eggs}} = 34\right)$ than for those from the *C. sepium* line $\left(\bar{X}_{\text{eggs}} = 27\right)$. Similarly, the population growth rate λ was 71 % higher for the *C. varians* population reared on *C. arvensis* ($\lambda = 3.01$, 95 % CI 2.96–3.05) than for the population reared on *C. sepium* ($\lambda = 2.13$, 95 % CI 2.05–2.20). Differences in λ were mainly explained by the contribution of the larva to pupa transition (Fig. 5); the pupa to adult transition and the fecundity term explained most of the remaining variance.

Discussion

Insect preference

Results from the choice experiment show that adult beetles prefer to feed on the host plant where their parents were raised. Thus, the mother's environmental experience is an important factor determining acceptability and preference of alternate hosts in *C. varians*. This trans-generational preference could explain, in part, the host fidelity (i.e., the tendency to feed on the same host species that it used in earlier life history stages) of this species, which feeds only on Convolvulaceae plants (Buzzi 1988; Windsor et al. 1992; Artigas 1973, 1994; Costa et al. 2007). Maternal preference has been shown to promote host fidelity in specialized insects by generating adaptive life history performance traits (Ruiz-Montoya and Núñez-Farfán 2009) and by maintaining a synchrony between insects and host plant phenology (van Asch et al. 2010) that reinforces the use of the original host. The pattern of host preference, however, was not equally strong between maternal feeding experiences. Given that beetles reared on *C. arvensis* chose 2.3 times more their original host as compared to only 1.5 of those reared on *C. sepium*, the former seems to show greater host fidelity. This divergence could be a result of differences in host quality given that *C. arvensis* is of higher quality than *C. sepium* (see next section). A proportion of individuals raised under a *C. sepium* maternal feeding experience could be choosing to feed on the alternative host, *C. arvensis*, where insect performance is enhanced. Because selection should favor individuals that preferentially choose hosts that are nutritionally best for growth, reproduction and survival (Thompson 2005), adult beetles may prefer an alternate environment if it enhances their own fitness.

Insect performance

Consistent patterns of host preference across generations are only a first step toward generating adaptive life history responses (Mousseau and Dingle 1991). Maternal preference is sometimes linked to the resulting performance of offspring (Gripenberg et al. 2010). In *C. varians,* the link between preference and performance is complex because of the context-dependent nature of the relation. Thus, individuals that come from parents raised on *C. arvensis*

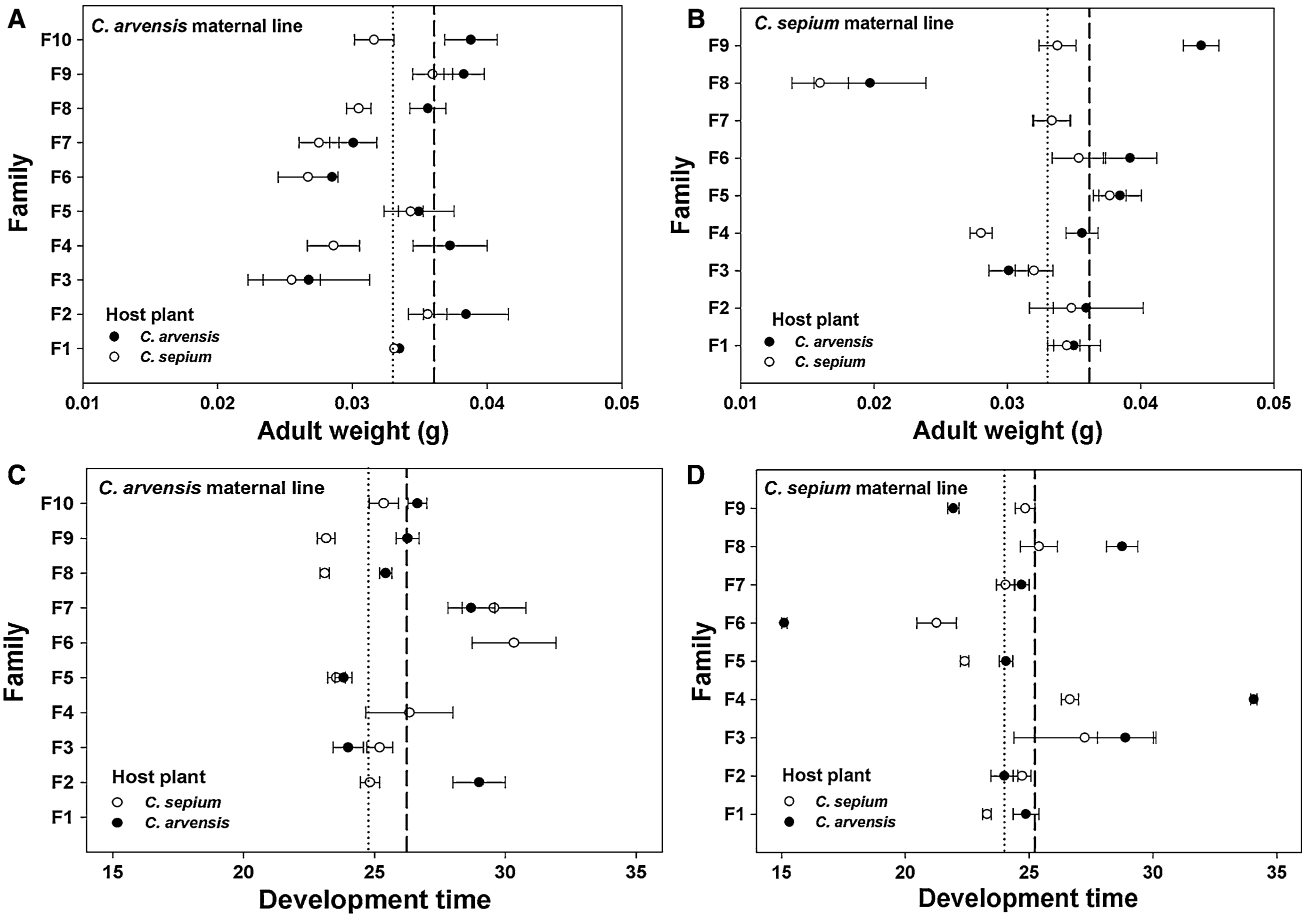


Fig. 3 Genetic variation in life history performance traits associated with maternal feeding experience and plant host treatments (F2 generation). *Left* panels (**a** and **c**) correspond to families coming from parents raised on *C. arvensis* leaves, and *right* panels (**b** and **d**) to families coming from parents raised on *C. sepium* leaves. *Open circles* correspond to family offspring fed with *C. sepium* leaves and closed circles to families fed *C. arvensis* leaves. *Dashed* and *dotted vertical lines* indicate the mean values (±SE) across families of *C. arvensis* and *C. sepium*, respectively

Table 1 Regression models showing estimates of the association between life history performance traits within host plant treatment

Host plant treatment	Pseudo-R^2	df	−Log L	*L-R* test (X^2)	*P*	Intercept β_o ± SE	Development time β_1 ± SE
C. arvensis	0.13	1	1.09	2.18	0.14	0.048 ± 0.009	−0.0005 ± 0.0003
C. sepium	0.23	1	2.50	5.00	0.03	0.061 ± 0.012	−0.0012 ± 0.0004

In both cases, adult weight is used as the response variable and development time as a predictor. Models were fitted using general linear models and significance is based on likelihood ratio tests (*L-R*)

show high preference for this host species, resulting in large body sizes. It has been shown that adult size is strongly correlated with fitness in insects (Honêk 1993; Nylin and Gotthard 1998). Moreover, these patterns support the idea that offspring size reflects a strong preference–performance relationship in herbivorous insects (Leather and Awmack 2002). Preference and performance are coupled in this case and can act synergistically to increase a fitness component, discouraging host switching and contributing to specialization. Offspring from parents raised on *C. sepium*, however, shows a different trend. For these beetles, preference and performance are decoupled, acting in opposite directions. Although individuals show preference for *C. sepium*, this preference translates into smaller body sizes, potentially producing maladapted individuals. Thus, in this case, preference and performance are decoupled, reducing a fitness component, encouraging a host switch and promoting generalization.

While in *C. varians,* maternal preference for a particular host seems to be transferred to the next generation, there was no evidence to suggest that maternal experience itself influences offspring performance directly, as has been shown in other systems (Mousseau and Dingle 1991). Host plant preference influences offspring body size only

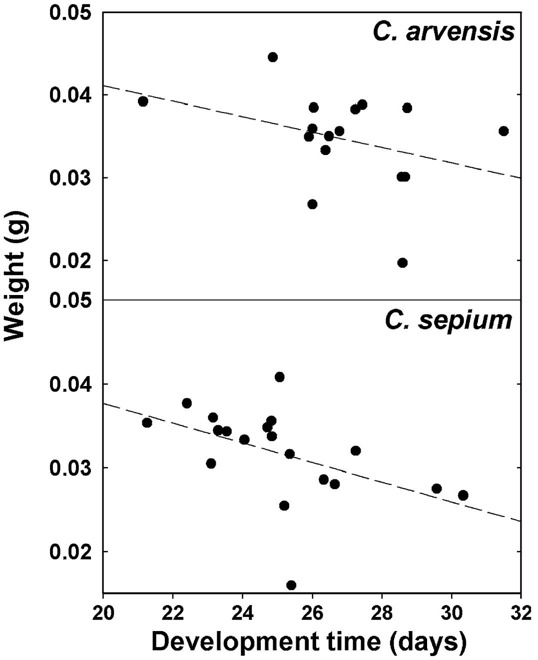
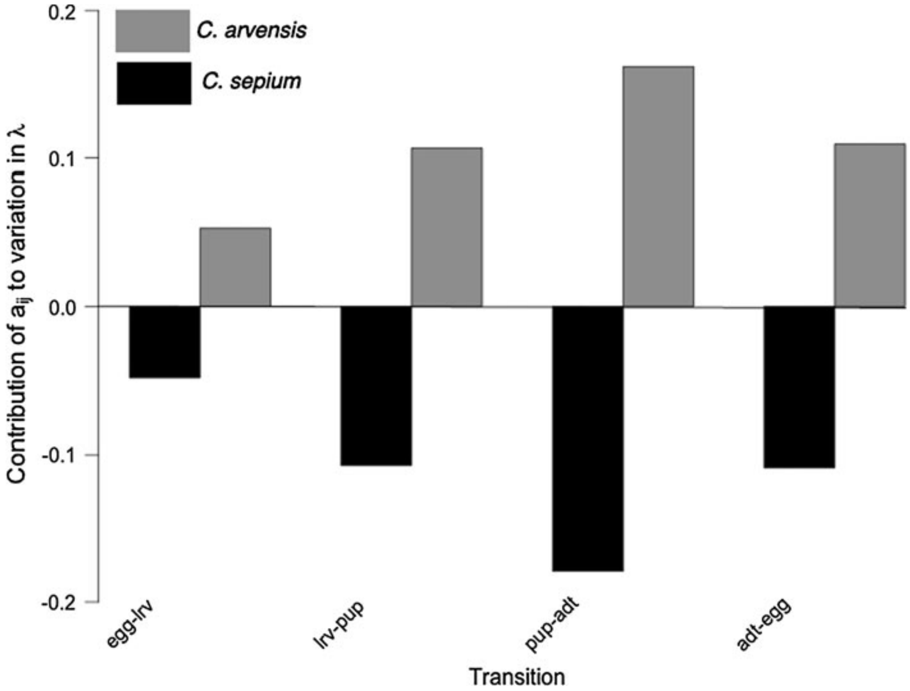


Fig. 4 The relationship between adult weight and development time in *C. varians* beetles on two host plants. Each *dot* is a mean family value and dashed lines correspond to fitted GLM models (see Table 1 for estimate values)

through a host plant effect. Thus, size differences in the experiment suggest that the preference–performance outcome is host dependent, where host preference will only contribute to adaptive life history responses if the original host is of better quality than an alternate host; otherwise, inherited host fidelity could be disadvantageous for the offspring generation. Accordingly, maternal host experience may not be a primary selective factor driving the life history responses in this species. Other studies have also found that host plant quality rather than maternal experience influences offspring performance directly (Via 1991; Solarz and Newman 2001; Kühnle and Müller 2011).

Optimal adult size can theoretically be achieved either via fast growth or by prolonging the growth period (Gotthard 2008). In *C. varians*, a host plant × maternal feeding experience interaction on development time appears to be triggering both growth strategies. First, beetles from a *C. arvensis* maternal feeding experience that fed on *C. arvensis* achieved large adult sizes by way of prolonged growth resulting in an efficient growth strategy. In contrast, when these larvae were fed *C. sepium*, they developed faster but produced adults of smaller size, thus decreasing performance after host switch. Second, beetles from a *C. sepium* maternal feeding experience that fed on *C. sepium* reached adulthood by fast growth, but adults reached small body sizes. When these larvae were fed *C. arvensis,* development time increased, but adults were of smaller size. Therefore, at least in laboratory conditions, prolonged growth may be an adaptive life history strategy for *C. varians* beetles, provided that both the maternal feeding experience and the feeding host is *C. arvensis*. Furthermore, there was no influence of development time on adult size when individuals fed on *C. arvensis*. In contrast, when individuals fed on *C. sepium*, adult size was constrained by an increase in developing time. Selection should favor individuals that balance fitness costs and benefits that lead to adaptive growth strategies (Abrams et al. 1996, Nylin

Fig. 5 Transition matrix element (A_{ij}) contributions to variation in λ for *C. varians* beetle populations reared on *C. arvensis* and *C. sepium*. Egg-lrv = transition from egg to larva, Lrv-pup = transition from larva to pupa, Pup-adt = transition from pupa to adult and Adt-egg = transition from adult to eggs of the next generation



and Gotthard 1998). Therefore, when individuals feed on *C. sepium*, rapid growth should be an optimal growth strategy because large body size is correlated with high reproductive output. Reaching the optimal size on *C. sepium* is, thus, directly linked to an interaction between life history performance traits. Such an interaction is not evident in individuals that feed on *C. arvensis*. Moreover, under field conditions, rapid development in *C. varians* could be more advantageous as it decreases exposure time of larvae and pupae to attack by natural enemies and/or abiotic stress (Fordyce and Shapiro 2003; Medina et al. 2005). High levels of larval parasitism by Tachinidae flies ($\sim$80 %) have been reported for this species under natural conditions (Olivares-Donoso et al. 2000).

The patterns described above demonstrate that, through differences in the interaction between life history performance traits, beetles will respond differentially to an alternate host plant. How *C. varians* responds will depend on the host plant effects on life history performance traits. Moreover, development time and adult size in *C. varians* showed considerable genetic variation under both host plant and maternal feeding experience treatments. Therefore, they can potentially generate adaptive life history responses that balance growth rates with body size in response to selective pressures (Gotthard 2008). It has been shown that individual larvae may adjust their growth trajectories in relation to information provided by the host plant (Gotthard 2004). If responses are adaptive, changes in the interaction between preference and performance can have important implications for host switching or colonization of alternative environments.

Effects of plant host on population growth of *C. varians*

The projection matrices describe how the host plant affects the demographic parameters in *C. varians* populations. Because $\ln(\lambda) = r$, the instantaneous population growth rate, lambda, can also be interpreted as the average fitness of the population in a given plant host environment (Charlesworth 1980; Caswell 2001). In our study, matrix projections revealed large differences in lambda between beetle populations reared in *C. sepium* and *C. arvensis*. Although both populations of *C. varians* showed positive growth, the population reared on *C. arvensis* plants had higher fitness than the population reared on *C. sepium*. Compared to *C. arvensis*, *C. sepium* had an overall negative effect on all transitions of *C. varians* life cycle, but particularly on the pupa to adult transition, which greatly declined in the *C. sepium* environment. These patterns suggest that changes in the preference–performance relationship can impact population dynamics of *C. varians* in different ways. If beetles prefer the host plant where their progeny performs best, that is, *C. arvensis*, life history responses will increase population growth and life stage transitions will contribute to positive population dynamics. However, if beetles prefer the host plant where their progeny performs worse, that is, *C. sepium*, life history responses and life stage transitions will contribute less to overall population growth.

Ecological and evolutionary implications

The data presented here show that individuals of *C. varians* prefer and/or perform differently on one host plant than another. Host experience of the parents strongly influences feeding preference of adult progeny. Earlier work showed that *C. varians* larvae were able to orient themselves to their feeding site (*C. sepium* leaves vs. moistened papers; Costa et al. 2007). The ecological and evolutionary consequences of this feeding preference, however, will depend on its link to life history performance traits that confer fitness advantages. For example, correlations mediated by means of linkage disequilibrium (e.g., Hawthorne and Via 2001; Via and Hawthorne 2002) between host preference and performance traits could be maintained through the effects of maternal host experience. This process could ultimately result in a scaling process that facilitates adaptation to a given host and, eventually, speciation if maternal preference strongly determines the host for offspring development (Wade 1998; Diehl and Bush 1989). We found evidence for such a link among individuals that come from a *C. arvensis* maternal line. These beetles show high preference for their maternal host, and this translated into high performance and an increase in potential fitness (larger size). Moreover, there is ample genetic variation in life history performance traits, among families within maternal lines. This variation potentially contributes to an increase in the degree of adaptation to a particular host by increasing the possibility of evolutionary change. Thus, there is great potential for phenotypic divergence in performance between individuals that are exploiting different host in this species.

Acknowledgments Research fellowships of M. Cárdenas and K. González at Universidad de Concepción (Chile) were funded by PER: 02 Project, International Science Programme, Uppsala University (Sweden). R. S. Ríos and A. P. Loayza were supported by MECESUP postdoctoral scholarships at Universidad de La Serena (Chile). The study was greatly improved by valuable comments from G. Stotz and C. Salgado-Luarte and two anonymous reviewers.

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