

Choosy mothers pick challenging plants: maternal preference and larval performance of a specialist herbivore are not linked

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Abstract. 1. Maternal preference is a dynamic process and interactions between preference and performance are fundamental for understanding evolutionary ecology and host association in insect–plant interactions. In the present study, the hypothesis of preference–performance was tested by offering solanaceous specialist *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae) larvae and adult females four plant congeners that ranged in suitability.

2. Larval feeding, development, oviposition, plant glycoalkaloids, and headspace volatiles in the four plant species were analysed to examine the extent of variation, which might explain performance–preference differences.

3. It was found that larval performance was mismatched with adult oviposition preferences. Adults laid more eggs on *Solanum immite* Dunal plants, which were poor hosts for larval development, feeding, and survival, compared to the other three *Solanum* species.

4. Chemical plant defenses, in general, did not correlate with performance or preference, but some plant volatiles may have played a role in resolving female choice. Glycoalkaloids such as solanine and chaconine were detected in similar amounts in preferred and non-preferred hosts, but there was significantly more limonene in the headspace of *S. immite* than in *S. tuberosum* L.

5. The present findings suggest that we must consider the risk-spreading hypothesis in cases where preference and performance are not positively correlated, particularly in specialist herbivores that can feed on a diversity of congener plants and may attempt to expand their exploits to other solanaceae species.

Key words. Glycoalkaloid, *Leptinotarsa decemlineata*, oviposition preference, plant–insect interactions, preference–performance hypothesis.

Introduction

The evolutionary adaptation theory assumes that an individual's fitness is a function of some aspect of its behaviour, morphology, etc., and that selection favours the expression of traits corresponding to a local maximum in fitness (Thompson, 1988). Herbivore fitness can differ drastically from one host species to the next (Denno, 1983). Indeed, we find that the overwhelming majority of insects have specialised rather than generalised

diets, which coincides with improved performance and efficiency (Schoonhoven *et al.*, 2005; Ali & Agrawal, 2012). When we examine factors that link performance on specific plants, we assume herbivores favour plants on which both they and their offspring perform best. The preference–performance hypothesis, also known as the ‘mother knows best’ principle (Valladares & Lawton, 1991), addresses host plant suitability in the context of maternal choice. Specifically, the hypothesis predicts that adult oviposition preference corresponds to offspring performance (Jaenike, 1978; Thompson, 1988). Thus, females are assumed to maximise their fitness by ovipositing on plants that will provide a high-quality diet for their offspring.

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A discrepancy between host plant quality and oviposition choice is not uncommon in insects (Courtney & Kibota, 1990). The risk-spreading (i.e. bet-hedging) hypothesis maintains that in unpredictable environments variance in fitness, even at the cost of lower mean fitness, is evolutionarily favoured (Levins, 1962; Cohen, 1966; Gillespie, 1974; Hopper, 1999). For example, when the risk of parasitism is unpredictable, and both inferior and superior host plants are available, *Pieris napi* L. adults laid more eggs on lower-quality plants compared to higher-quality plants (Ohsaki & Sato, 1994). Depending on the insect species, mothers may compensate for lower plant quality by laying a few high-quality eggs or a large number of poor-quality eggs (Awmack & Leather, 2002). This risk-spreading behaviour requires variation in plant quality, decoupling of adult feeding preference, and oviposition preference, and species where larvae are relatively immobile, and adults feed on similar host plants as the offspring.

Variation in host plant quality often arises from plant metabolites and volatile organic compounds (VOCs), which are variable within and among plant species (Bernays & Chapman, 1994; Paré & Tumlinson, 1999). Specialised plant metabolites have repeatedly been shown to affect larval and adult herbivore performance (Rosenthal & Berenbaum, 1992; Karban & Baldwin, 1997), but less is known about their impact on oviposition choice (Feeny *et al.*, 1983; Bernays & Chapman, 1994; Städler, 2002). The bet-hedging strategy in ovipositing females can be explained if, for example, larvae sequester toxic metabolites from chemically defended plants (Awmack & Leather, 2002).

Solanaceous plants are a good example of a system where there is considerable variation in plant quality; these plants contain glycoalkaloids, a group of steroidal compounds that can be toxic to some insects (Friedman & McDonald, 1997). The intra-family variation among solanaceous plants for glycoalkaloids (Friedman, 2006) and the response of the specialist herbivore *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae), Colorado potato beetle, to these metabolites varies greatly (Hsiao & Fraenkel, 1968; Flanders *et al.*, 1992; Hollister *et al.*, 2001). This insect is the most economically significant defoliator of potatoes (*Solanum tuberosum* L.) in northern latitudes across the globe and insecticides are the main mode of controlling them (de Wilde & Hsiao, 1981; Ferro, 1985). Alternative management strategies, such as plant resistance, are gaining attention because of the rise in insecticide resistant *L. decemlineata* populations (Casagrande, 1987). Glycoalkaloids in *Solanum chacoense* Bitter have been associated with resistance to *L. decemlineata* and efforts have focused on using these secondary metabolites for pest management (Sinden *et al.*, 1986; Lawson *et al.*, 1993). The qualitative aspect of plant volatile blends is also important for *L. decemlineata* host location: adding odours from non-host solanaceous species, such as *Solanum habrochaites* (S.Knapp & D.M.Spooner) (wild tomato) into the odour blend stopped *L. decemlineata* from responding to potato odour (Thiery & Visser, 1986). Such chemical diversity in plant metabolites in Solanaceae provides an opportunity to improve our understanding of preference–performance strategies in herbivores.

Here we test the preference–performance hypothesis in *L. decemlineata* by measuring responses of this insect when

exposed to single accessions of three wild *Solanum* species: *S. chacoense* Bitter, *S. immite* Dunal, *S. pinnatisectum* Dunal, and the cultivated potato *S. tuberosum* L. cv. Atlantic. We determined performance by measuring larval survival, feeding, and development and, we evaluated the adaptiveness of female preference by measuring oviposition of *L. decemlineata* when simultaneously exposed to the four plant species in choice experiments. Finally, the allelochemical (glycoalkaloid) and VOC contents in the four plant species were analysed to determine how variation in resource quality relates to oviposition preference and larval performance.

Materials and methods

Insect and plant material

Leptinotarsa decemlineata larvae and adults used in all the experiments were obtained from a laboratory colony maintained at the Vegetable Entomology Laboratory at Michigan State University (East Lansing, Michigan). The colony was kept in continuous culture on *Solanum tuberosum* cv. Atlantic in a rearing room at 25 °C and 16:8 (L:D) photoperiod.

The plant species we tested were *S. chacoense*, Bitter (PI 123123, selection 3), *S. immite*, Dunal (PI 365330, selection 3), and *S. pinnatisectum*, Dunal (PI 184774, selection 88), obtained from the United States Potato Genebank (NRSP-6, Sturgeon Bay, Wisconsin). These species originate from different countries, occur at different altitudes, and have different levels of insect and disease resistance (Table S1). *Solanum tuberosum* L. cv. Atlantic, the cultivated potato was obtained from plants grown at the Montcalm Potato Research Farm (Stanton, Michigan). These species were selected for this study because of their value for plant breeding as potential sources of resistance to pests, like *L. decemlineata*.

All plants were vegetatively propagated and grown in an environmental chamber at 25 °C, 75% RH, 14:10 (L:D), planted in 12-cm diameter plastic pots in a perlite soil mix (Suremix Perlite, Michigan Grower Products Inc., Galesburg, Michigan). Plants were fertilised weekly with a 5 g l⁻¹ 14-10-14 N-P-K (Scott's, Miracle-Grow Products, Inc. Marysville, Ohio) solution.

Larval foliage consumption

Foliage consumption by larvae was compared in a no choice experiment. The youngest fully expanded leaf was collected from different 4–5-week-old plants for each no choice trial. To prevent desiccation, each leaf petiole was placed in a 1.7-ml water-filled plastic microcentrifuge vial with a perforated cap. Individual leaves were placed in plastic Petri dishes (90 × 15 mm²) on moist filter paper (Whatman #1, VWR, Radnor, Pennsylvania). The leaf area (cm²) was obtained using a Li-Cor Portable Leaf Area Meter (LI-3000C, Lincoln, Nebraska). Newly ecdysed second instar *L. decemlineata* were starved for 4 h preceding the assay, and one larva was placed in each Petri dish. Petri dishes were held at 25 °C, 70–75% RH, 16:8 (L:D) for 48 h. The water in the microcentrifuge vials was

checked twice daily and refilled when necessary. At the end of the 48-h period larvae were removed, leaves were rinsed using tap water to eliminate excreta, wiped dry, and scanned again to record the final leaf area. This experiment was repeated with 10 replications on two different dates (05 August 2014 and 22 August 2014) using new groups of larvae and plants each time ($N = 20$ per plant species).

Larval foliage consumption was calculated by subtracting the final leaf area from the initial leaf area. Data were evaluated using analysis of variance (ANOVA), and post-hoc means comparisons were done by Tukey's Honest Significant Different (HSD). This test and all subsequent statistical tests, unless noted otherwise, were performed using R (R version 3.2.2; R Core Team, 2015).

Larval survival

Egg masses were collected from the *L. decemlineata* colony and allowed to hatch at room temperature in Petri dishes. Five neonates (0–24-h old) from different egg masses were placed in the upper third of every potato plant using a paintbrush. The 4–5-week-old plants were covered with mesh (white polyester, 680- μm mesh aperture, Megaview, Taichung, Taiwan) and the mesh was secured with a string around the top of the pot to prevent larvae from escaping. To keep the mesh away from the plants, two metal wire hoops were bent over each pot with their ends inserted into the soil.

Infested plants were arranged in a randomised complete block design held at 25 °C, 70–75% RH, 16:8 (L:D) for 8 days. The numbers and developmental stages of living and dead larvae were recorded at the end of 8 days. The experiment was replicated twice (10 October 2014 and 11 November 2014) for a total of 10 replications per plant species with five larvae per plant, using a total of 200 larvae over the course of this assay. The number of larvae surviving after 8 days was analysed with a two-way ANOVA (plant species and block as factors) followed by Tukey's HSD procedure to determine differences among means ($\alpha = 0.05$).

Oviposition preference

The oviposition behaviour of mated *L. decemlineata* females on the four plant species was compared in choice tests. One 5-week-old plant of each species was organised randomly in the four corners of a 0.6 \times 0.6 \times 0.6 m³ square collapsible metal cage (BioQuip Products Inc., Rancho Dominguez, California). Plants were chosen so that the four plants in a cage were matched for size. Ten cages were organised in a completely randomised design and kept on lab benches at 22–25 °C, 70–75% RH and 16:8 (L:D). At the start of the experiment, one mated female (approximately 8–10 days post-emergence) was released in the centre of each cage. Plants were inspected for new egg masses daily for 4 days, without removing the egg masses from the plant. At the end of the 4 days, the total number of egg masses and the number of eggs per egg mass were counted. Egg masses laid anywhere other than plant tissue were omitted from the

analysis. The entire experiment was replicated twice, once in 2014 and once in 2015, for a total of 20 replications.

Differences in the total number of egg masses and the total number of eggs among potato species were compared using a Kruskal–Wallis test followed by Dunn's test for post-hoc means comparison ($\alpha = 0.05$). The average number of eggs per egg mass was compared with an ANOVA followed by Tukey's HSD procedure to determine differences among means. The cumulative number of egg masses was compared with a χ^2 test by day across species.

Plant tissue analysis

Glycoalkaloid analysis was done on 4-week-old undamaged plants. Ten plants were used per species, and one leaflet from the top third part of each plant was collected for extraction. The tissue (100 mg) was pulverised in liquid nitrogen, and 1 ml of extraction solvent (water, methanol and acetic acid, 49:49:2 v/v/v) was added. The samples were then heated at 60 °C in a water bath for 30 min, followed by centrifugation at 21 130 g for 20 min and then the supernatant was transferred to a 2-ml glass vial. Samples were analysed with a Waters G2-XS QToF liquid chromatograph-mass spectrometer (MS) interfaced to a Waters Acquity Ultra Performance Liquid Chromatography system using a method described previously (Schillmiller *et al.*, 2015). A non-targeted analysis of peaks from the lowest collision energy function was performed using Waters Markerlynx XS (Version 3.0.1, Waters Corp.). Masses between m/z 50 and 1500 were included using a mass window of 0.05 and a marker intensity threshold of 5000 counts. Filtering was performed to remove masses that had a fractional mass above 0.7. Peak areas of alkaloids were averaged across 10 replicates for each species. Peak areas of all detected glycoalkaloids were analysed using non-metric multidimensional scaling and an analysis of similarity (ANOSIM, $\alpha = 0.05$) to determine overall glycoalkaloid profile differences among species. Peak areas of chaconine, solanine, and tomatine were compared among the four plants with ANOVA followed by Tukey's HSD ($\alpha = 0.05$).

Headspace analysis

Volatile organic compound collection from the four *Solanum* species ($n = 6$: *S. chacoense*, *S. immite*; $n = 7$: *S. pinnatisectum*, *S. tuberosum*) was conducted in the same growth chamber where plants were grown (25 °C, 75% RH, 14:10 L:D). Undamaged 4–5-week-old plants were individually placed into closed glass chambers (18 cm diameter, 38 cm height). The soil and pot were covered with aluminum foil to minimise odour contamination of the headspace. A vacuum pump pulled air from the chambers through a Super Q trap (50/80 mesh; Alltech, Deerfield, Illinois; 30 mg in a 150 mm by 50 mm glass tube) for 6 h at a rate of 1 l min⁻¹. The air was allowed to enter the chamber through a charcoal filter. Volatiles were extracted from the Super Q trap using 150 μl of methylene chloride. The volatile extracts were analysed on an Agilent 7890 A gas chromatograph (GC) equipped with a HP-5MS Agilent J&W column (30 m length, 250 μm diameter and 0.25 μm film thickness, He as the carrier

gas at constant 1 ml min⁻¹ flow) coupled with an Agilent 5975C inert XL MS. Compounds were separated by injecting 1 µl of sample into the GC/MS. The GC oven temperature programme consisted of 35 °C for 1 min followed by 10 °C min⁻¹ to 260 °C then hold at 260 °C for 6.5 min. After an initial solvent delay of 4 min, masses between *m/z* 40–550 atomic mass units were scanned.

Volatile organic compounds separated by GC/MS were processed with the Automated Mass Spectral Deconvolution and Identification System [AMDIS, Version 2.70; National Institute of Standards and Technology (NIST), Gaithersburg, Maryland]. A library of 37 known compounds was compiled with AMDIS using the NIST database as a reference. The AMDIS report was processed with the 'Metab' R package (Aggio *et al.*, 2011). Data were normalised to the internal standard, by fresh plant biomass and hour of collection to calculate volatile emission per sample (ng g⁻¹h⁻²). Headspace composition was then compared among the four plant species using non-metric multidimensional scaling and an analysis of similarity (ANOSIM). The quantities of limonene, copaene, nonanal, methyl salicylate, and caryophyllene were compared in the four plant species using ANOVA followed by Tukey's HSD ($\alpha = 0.05$). These five compounds were identified using the comparison of their retention times and spectra to standards.

Results

Larval foliage consumption

Leaf area consumed by a second instar during 48 h was significantly different among the plant species ($F = 28.98$, d.f. = 3,74, $P < 0.01$), ranging from 1.16 to 8.61 cm² (Fig. 1). Leaf area consumed by larvae was approximately five-times lower on *S. immite* compared to the other plant species. *Solanum immite* and *S. pinnatisectum* had on average 75% less larval feeding than either on *S. tuberosum* or *S. chacoense* (all $t > 1.69$, d.f. = 74, $P < 0.05$). After 48 h, all larvae that fed on *S. chacoense* and *S. tuberosum* were third instars, whereas all larvae feeding on *S. immite* and *S. pinnatisectum* remained in the second instar. No larval mortality was observed during the 48-h period.

Larval survival

Larvae confined on the four *Solanum* species for 8 days had significantly different survival ($F = 29.43$, d.f. = 3,25, $P < 0.01$; Fig. 2). Larval survival was three-times greater on *S. chacoense* and *S. tuberosum* than on *S. immite* ($t > 7.48$, d.f. = 25, $P < 0.01$). On average, only 20% of the larvae survived on *S. pinnatisectum* after 8 days. Larvae that survived on *S. pinnatisectum* were still second instars after 8 days, but larvae on *S. chacoense* and *S. tuberosum* were all fourth instars.

Oviposition preference

The number of eggs per mass was significantly different among the four plant species ($\chi^2 = 9.34$, d.f. = 3, $P = 0.03$;

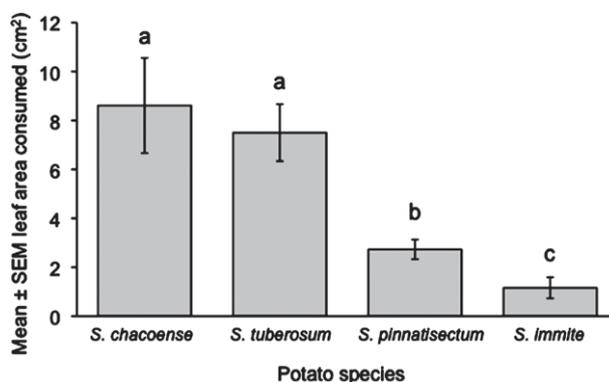


Fig. 1. The mean (\pm SEM) leaf surface area (cm²) of four *Solanum* species consumed by second instar *Leptinotarsa decemlineata* during 48 h of feeding. Different letters above bars denote significant differences among means [Tukey's Honest Significant Different (HSD), $P < 0.05$].

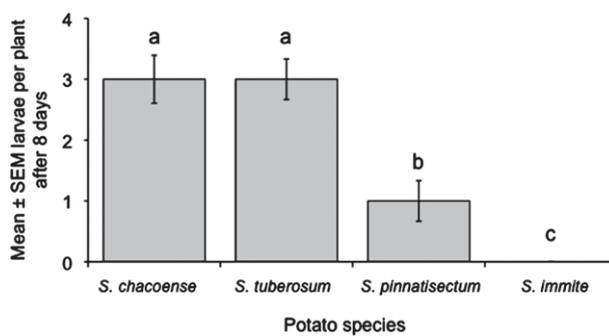


Fig. 2. The mean (\pm SEM) survivorship of *Leptinotarsa decemlineata* larvae on four *Solanum* species after 8 days; five neonates were placed on each plant at the beginning of the trial. Different letters above bars denote significant differences among means [Tukey's Honest Significant Different (HSD), $P < 0.05$].

Fig. 3a). *Solanum immite* received the most egg masses, approximately 40–50% more than *S. chacoense* or *S. pinnatisectum* ($\chi^2 > 2.52$, d.f. = 3, $P < 0.01$). *Solanum tuberosum* received 37% fewer egg masses than *S. immite* ($\chi^2 = 2.39$, d.f. = 3, $P < 0.01$). In terms of the total number of eggs, *S. immite* received about 70% more eggs than *S. chacoense* or *S. pinnatisectum* ($\chi^2 > 2.84$, d.f. = 3, $P < 0.01$, Fig. 3b). *Solanum tuberosum* had 2.24 times fewer eggs than *S. immite* ($\chi^2 = 2.61$, d.f. = 3, $P < 0.01$).

The average number of eggs per egg mass was similar on *S. chacoense* and *S. tuberosum* at 7 eggs/mass ($t = 0.01$, d.f. = 19, $P = 1.00$), but egg masses on *S. immite* had 32 eggs/mass, significantly more than on any of the other three species (all $t > 3.12$, d.f. = 19, $P < 0.05$; Fig. 3c). In the first 2 days of the assay, 65–90% of the total egg masses were laid on *S. immite*, *S. chacoense*, and *S. pinnatisectum*, whereas 46% were laid on *S. tuberosum* (Fig. 3d). Significant differences among the cumulative number of eggs appeared on the second day of the experiment and egg numbers remained the highest on *S. immite* until the end of the experiment ($\chi^2 > 7.09$, d.f. = 3, $P < 0.01$; Fig. 3d).

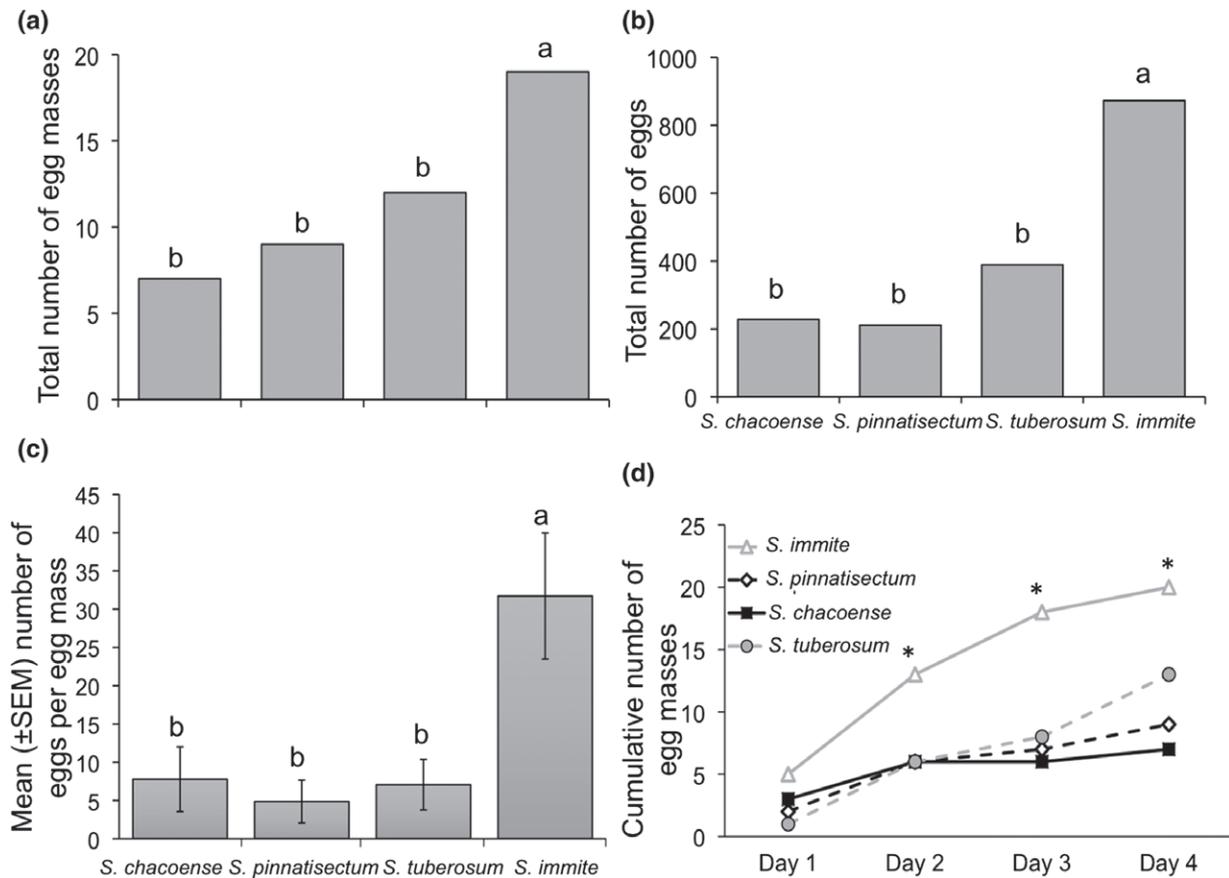


Fig. 3. Oviposition preference of *Leptinotarsa decemlineata* females in a four-choice test, (a) total number of *L. decemlineata* egg masses, (b) total number of eggs laid, (c) the mean (\pm SEM) number of eggs per egg mass and, (d) the cumulative number of egg masses over 4 days on four *Solanum* species. Different letters above bars and asterisks denote significant differences among means ($P < 0.05$).

Plant tissue analysis

The glycoalkaloid profiles significantly differed across plant species (ANOSIM: $R^2 = 0.94$, $P < 0.01$; Fig. 4a). Chaconine and solanine were detected in *S. chacoense*, *S. immite*, and *S. tuberosum*, but not in *S. pinnatisectum* (Fig. 4b). In contrast, tomatine was present only in *S. pinnatisectum*. The amount of chaconine and solanine was similar in *S. immite* and *S. tuberosum* (all $t > 13.75$, d.f. = 36, $P < 0.01$) but it was approximately 20–50% less in *S. chacoense* than in the other two species (all $t > 13.75$, d.f. = 36, $P < 0.01$).

Headspace analysis

A comparison of 37 compounds revealed significant differences among the four species' headspace composition (ANOSIM: $R^2 = 0.29$, $P < 0.01$; Fig. 5a). The quantities of limonene, copaene, methyl salicylate, and caryophyllene were significantly different among the four species (all $F > 3.26$, d.f. = 3,22, $P < 0.05$; Fig. 5b). On average, we found 25-times more limonene in *S. immite* than in *S. tuberosum* ($t = 2.96$, d.f. = 22, $P = 0.03$). In contrast, there was approximately four-times as much copaene in *S. tuberosum* than in *S. immite*

($t = 3.48$, d.f. = 22, $P = 0.01$). The amount of methyl salicylate and caryophyllene was 2.5–5-times greater in *S. chacoense* than in the other three species (all $t > 4.70$, d.f. = 22, $P < 0.01$). The quantity of nonanal was not significantly different among the four species ($F = 2.59$, d.f. = 3,22, $P = 0.08$; Fig. 5b).

Discussion

While the majority of cases reported in the literature offer clear support for the preference–performance hypothesis (Jaenike, 1978; Gripenberg *et al.*, 2010), there are also plenty of examples for insects making non-adaptive decisions when laying eggs (Hsiao & Fraenkel, 1968; Bongers, 1970; Chew, 1977; Courtney & Kibota, 1990; Valladares & Lawton, 1991; Benda *et al.*, 2011). The relationship between maternal preference and larval performance in *L. decemlineata* was poorly matched in our laboratory experiments, and it remains unclear if female oviposition choice is unrelated to plant chemistry.

Preference–performance decoupling

As *L. decemlineata* specialises on plants in the genus *Solanum*, we hypothesised that oviposition behaviour will be closely

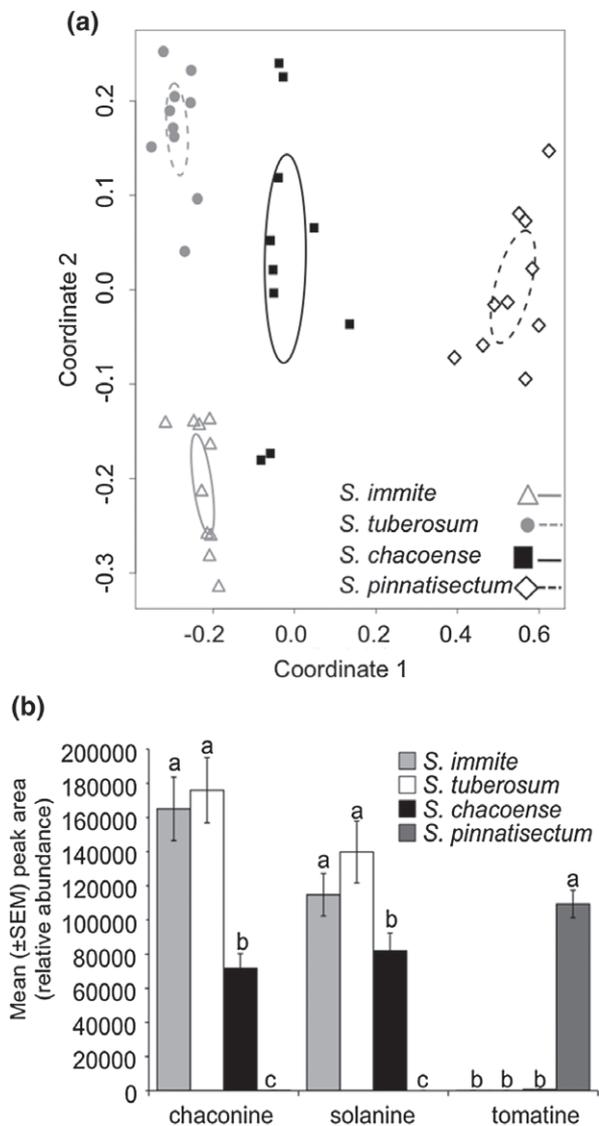


Fig. 4. Non-metric multidimensional scaling with leaf total glycoalkaloid content of four *Solanum* species (a). The mean (\pm SEM) peak area of three different leaf glycoalkaloids (chaconine, solanine, and tomatine) in the four *Solanum* species (b). Different letters above bars denote significant differences among means [Tukey's Honest Significant Different (HSD), $P < 0.05$].

aligned with larval performance (Gripenberg *et al.*, 2010); instead, we found evidence for the 'bet-hedging' strategy. While larvae performed best on *S. tuberosum* and *S. chacoense*, females preferred to lay eggs on *S. immite*, a plant that caused the highest larval mortality. Previous findings in *L. decemlineata* oviposition have provided mixed results. When given a choice among plants, the numbers of eggs were sometimes higher on ones that did not support larval or adult feeding (Hsiao & Fraenkel, 1968; Bongers, 1970; Sinden *et al.*, 1980). Contrary to this, there is also evidence for higher egg numbers on the plants that corresponded to high larval performance (Pelletier *et al.*, 2001). Thus, the present study and previous work provide evidence for a decoupling of female preference and larval performance when

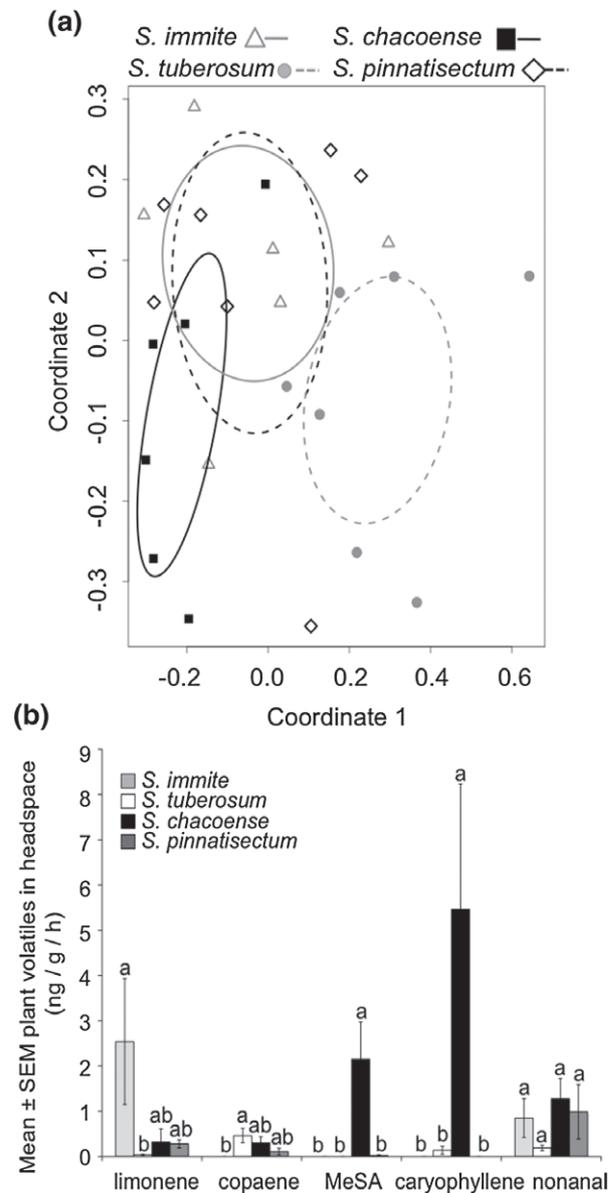


Fig. 5. Non-metric multidimensional scaling comparison of the total volatile profile of four *Solanum* species (a). The mean (\pm SEM) $\text{ng g}^{-1} \text{h}^{-2}$ emission for five specific volatile compounds by *Solanum* species, MeSA, methyl salicylate (b). Different letters above bars denote significant differences among means [Tukey's (Honest Significant Different HSD), $P < 0.05$].

females are offered a choice. Such conclusions follow findings of numerous studies that show mixed correspondence between preference and performance across systems (reviewed in Janz, 2002).

There are various evolutionary and ecological explanations for a mismatch between preference and performance; one possible explanation for its prominence in *L. decemlineata* is that it is predisposed for host range expansion (Hare & Kennedy, 1986). In general, acquiring new host plants can be because of external stimuli, such as the avoidance of natural enemies (enemy-free

space) or differential availability of food, neither of which conditions were present in our lab choice tests. In the absence of external selective pressures, a wider adult and a narrower larval host range may be an evolutionary strategy for widening the host range (Wiklund, 1974). Any surviving larvae on a low-quality host plant will have access to a new niche that will reduce, for example, intraspecific competition; this is especially beneficial if larvae use multiple plants to complete their development. In our experiments, females may have laid larger egg masses on *S. immite* to minimise losses because of intra-clutch cannibalism that can be greater on poor-quality host plants (Collie *et al.*, 2013; Baker *et al.*, 2014). Within-generation risk spreading is another explanation for the observed pattern, where females spread risks among different patches of host plants (e.g. four plants in a cage) (Thompson, 1988). This could be the case here, as *L. decemlineata* females accepted *S. pinnatisectum* for egg laying, a plant that significantly reduced larval survival compared with *S. tuberosum*, and all the plants in the choice test were accepted for oviposition. When novel plants are offered to insects, females sometimes accept them for oviposition (Chew, 1977), however, the fact that *L. decemlineata* females not only laid more eggs but also laid larger egg masses on *S. immite* may indicate a preference that goes beyond risk spreading or making oviposition ‘mistakes’, and can actually be an adaptive strategy for range expansion.

Plant chemistry and preference–performance

As secondary plant metabolites play an important role in insect host specificity (Sinden *et al.*, 1980; Tingey, 1984; Harrison & Mitchell, 1988; Feeny, 1992; Kowalski *et al.*, 1999; Hollister *et al.*, 2001), we hypothesized that the metabolite profiles for suitable oviposition and larval hosts will be similar. Contrary to our expectation, we found that the overall glycoalkaloid profiles were not related to oviposition or larval performance. For example, the number of egg masses laid on *S. chacoense*, *S. pinnatisectum*, and *S. tuberosum* was similar, but their glycoalkaloid profiles were qualitatively different from each other. However, larval feeding and development in our experiments were highest on plants that contained solanine and chaconine, the two secondary plant compounds that make up the majority of *S. tuberosum*'s glycoalkaloids (Friedman & McDonald, 1997; Friedman, 2006). While these two compounds serve in host recognition (Mitchell & Harrison, 1985), they are neutral to *L. decemlineata* performance (Sinden *et al.*, 1980; Lawson *et al.*, 1993; Kowalski *et al.*, 1999) and are not sequestered in the larval or adult stages (Armer, 2004). Low-foliage consumption by larvae on *S. immite* and *S. pinnatisectum* could have been caused by one or more deterrent or toxic compounds in leaves. Although it seems intuitive that well-defended plants will have a few specialised plant compounds with high biological activity, it is more often the case that plants tend to contain a high diversity of inactive secondary compounds, thus unique or abundant plant metabolites are not necessarily important in shaping insect–plant interactions (Jones & Firn, 1991). There is also evidence that the secondary metabolite content of plants change over time, so females may not have evolved an ability to choose the best plants for their offspring owing to the unreliability of

host cues especially in annual plants that can change quickly as they grow (Gripenberg *et al.*, 2007). For example, Anderson and Alborn (1999) found that *Spodoptera littoralis* laid more eggs on damaged younger plants than undamaged plants, but the preference switched when offered plants that were older.

We recovered some resolution of preference and performance with our observations of VOCs. Overall headspace profiles of *S. pinnatisectum* and *S. immite* were similar, and these were the two species least preferred for larval feeding. When examining some individual headspace VOCs, *S. immite* was different in that it emitted limonene in larger quantities than the other three species. Limonene is a well-known insect repellent with insecticidal properties (Ibrahim *et al.*, 2001). Although the role of VOCs in host plant recognition is well characterised in *L. decemlineata* (McIndoo, 1926; Visser *et al.*, 1979; Bolter *et al.*, 1997; Schütz *et al.*, 1997; Landolt *et al.*, 1999; Dickens, 2000) it is much less clear what role these play in oviposition choices of females. In general, it seems that most of what we know about the effect of VOCs on host plant selection is related to feeding and less to oviposition (Renwick, 1989), especially in insects where both adults and larvae feed on the same hosts [i.e. most oviposition behaviour work is done on Lepidoptera with foliar feeding larvae and nectar-feeding adults (reviewed in Hilker & Meiners, 2002a)]. Furthermore, little is understood about whether the VOCs that are used in food resource finding are the same ones that are used in finding plants for oviposition. One interesting explanation for the observed results is related to the fact that plants produce defensive volatiles when eggs are deposited on them; some herbivores sense these and avoid plants with eggs (Hilker & Meiners, 2002b). It is possible that oviposition-induced plant volatiles are unfamiliar or unrecognised on a new host plant, which may result in more eggs deposited on a novel host.

Synthesis

Among plant congeners, it is expected that some generalised hosts cues be shared while maintaining some level of dissimilarity. Generalised host cues may not always be reliable indicators of host quality, and may be the cause for a decoupling of preference and performance. The preference–performance hypothesis also assumes that larvae cannot disperse (Clark *et al.*, 2011), but many larvae, including beetles, can relocate to nearby plants. Thus, mothers of these somewhat mobile larvae may be less choosy especially if a suitable plant for larval development is nearby. Maternal preference is indeed a dynamic process, and the relationship between oviposition preference and offspring performance is the essence of the problem of evolutionary ecology and specificity of host association in insect–plant interactions. Our current understanding of the preference–performance problem is preliminary, and studies such as this, which integrate plant traits and insect behavior, are key in resolving this relationship.

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M. H., J. A., and Z. S. conceived and designed the experiments. M. H., A. L. S., and Z. S. performed and analysed the experiments. M. H., A. L. S., J. A., and Z. S. wrote the manuscript.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/een.12350

Table S1. Some characteristics of the four *Solanum* species used in the present study.

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