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Adult host-plant preference and larval performance in an oligophagous insect (*Chnootriba elaterii*)

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Abstract

The present research investigates host preferences and larval development of the melon ladybird *Chnootriba elaterii* (Rossi) (Coleoptera: Coccinellidae), considering seven Cucurbitaceae plant species (*Citrullus lanatus*, *Cucumis melo*, *Cucumis sativus*, *Cucurbita pepo*, *Cucurbita moschata*, *Lagenaria siceraria* and *Luffa aegyptiaca*), to determine whether mother host preference is related with larval performance. The damaged area on plant leaves due to insect feeding in dual-choice experiments was used to evaluate food preferences. Behavioural experiments in a Y-tube olfactometer tested the role of olfaction in host-plant selection. Parameters such as development duration and morphometric characters of emerged adults were evaluated to estimate larval performance. Adult females selected watermelon and melon as their favourite food while firmly refusing loofah and calabash. Insects preferred melon over watermelon, but the larval development on melon was slower; moreover, watermelon allowed larvae to develop faster than other tested plants, while loofah did not allow larval development. Larvae fed and developed on melon, pumpkin, zucchini, cucumber and calabash, without strong differences. These results only partially supported the preference-performance hypothesis suggesting that it could be context dependent. Contrary to expectation, volatile organic compounds (VOCs) belonging to the host, only partially could guide adult females in the olfactometer. This result suggests that long-distance olfactory stimuli alone cannot provide sufficient information for host-plant selection in melon ladybirds. Considering the economic relevance of *C. elaterii*, the results of the present paper answer some basic questions about host-plant selection for this pest insect, potentially useful to improve control strategies in crops.

KEYWORDS
African melon ladybug, behaviour, chemical ecology, Cucurbitaceae, life cycle, olfaction, preference-performance hypothesis (PPH), VOCs

INTRODUCTION

In herbivorous insects, the main behaviours affecting fitness, such as feeding, mating, and oviposition, are influenced by plant-related cues (Awmack & Leather, 2002; Carrasco et al., 2015; Städler et al., 2002; Wang et al., 2022). The success of an oligophagous herbivorous insect, in particular, depends on its ability to locate the best host plant, use its nutrients and cope with its defence (Bernays & Chapman, 1994; Fernandez & Hilker, 2007). The selection of host plants by insects is often performed by adults, particularly in species with low mobility larvae, whose performance depends significantly on the mother's host choice. In this context, the relationship between female preference

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and offspring performance is a central ecological question (Jaenike, 1978; Jones & Agrawal, 2019; Nardi et al., 2023); at an interspecific level, this is a critical factor in crop pest infestation (Berdegué et al., 1998). The 'preference-performance hypothesis' (PPH), also known as 'mother knows best' theory, has been widely investigated in the ecology of phytophagous insects and states that females preferentially lay their eggs on plants providing the best larval development (Menacer et al., 2021). This theory has been confirmed at intra and interspecific levels in many species, mainly Lepidoptera (Jones & Agrawal, 2019), but there are also several cases, some of them in Chrysomelidae Coleoptera (Jones & Agrawal, 2019), where the positive correlation between adult host preference and offspring performance does not exist (Berdegué et al., 1998; Hufnagel et al., 2017; Mayhew, 2001; Menacer et al., 2021; Valladares & Lawton, 1991). In particular, in insects that seem to be such poor mothers, this behaviour can be genuinely little adaptive, for example in exotic species that did not have time to adapt, or due to errors in cues perception (Mayhew, 2001). Still, it could be due to alternative adaptive strategies, such as mothers that choose host plants based on their own diet, selecting food that ensures their best survival and fecundity (Mayhew, 2001; Scheirs et al., 2000).

Insects use several cues in their host-finding process; in particular, volatile organic compounds (VOCs) emitted by plants are among the primary cues used by phytophagous to locate their host (Bernays & Chapman, 1994; Fernandez & Hilker, 2007; Hansson & Stensmyr, 2011; Harris & Miller, 1988; Piersanti et al., 2020; Prokopy & Owens, 1978; Rondoni et al., 2021; Saxena & Goyal, 1978; Sevarika et al., 2020; Vaishampayan et al., 1975). Numerous studies have been conducted on the attractiveness of host-plant volatiles on phytophagous beetles and several species of Chrysomelidae are reported as dependent from olfactory cues in their host-finding process (Fernandez & Hilker, 2007; Stenberg & Ericson, 2007).

Phytophagous ladybirds are among the most significant pests in Solanaceae and Cucurbitaceae crops, but still little is known about the host plants of these beetles (Stenberg & Ericson, 2007; Tomaszewska & Szawaryn, 2016) and some recent papers also report Poaceae, Urticaceae, Convolvulaceae, Fabaceae, and even Aristolochiaceae or Caryophyllaceae as host plants for some species (Beyene et al., 2007; Park & Yoon, 1991; Zhang & Ou, 2010). Among Epilachnini, the melon ladybeetle *Chnootriba elaterii* (Rossi) (Coleoptera: Coccinellidae) is one of the most injurious pests for cucurbit crops in the Mediterranean regions, North Africa, the Arabian peninsula and Iran (Akandeh et al., 2011; Al-Digail et al., 2012; Liotta, 1964). *C. elaterii* overwinters as adults close to the host cucurbit plant. In spring, females mate and lay eggs on the abaxial surface of the host leaves; newly hatched larvae are gregarious and do not stray far from the egg batches (Agrò et al., 2011; Liotta, 1964). Larvae and adults feed on the same Cucurbitaceae plants, attacking leaves but sometimes flowers and fruits (Akandeh & Shishehbor, 2011; Ali & Saeady, 1980; Liotta, 1964). This pest is also a vector of plant viruses and diseases (Bayhan & Bayhyan, 2017).

Some observations about food preferences among cucurbits and development on different host species have been reported for melon ladybird (Akandeh & Shishehbor, 2011; Ali & Saeady, 1980; Awadalla et al., 2011; Bayhan & Bayhyan, 2017; El-Abdin & Siragelnour, 1991; Wool & van Emden, 1981). Still, none of these research works investigated both aspects and they mainly focused on snake cucumber (*Cucumis melo* var. *flexuosus*), watermelon (*Citrullus lanatus*) and cucumber (*Cucumis sativus*), economically essential crops in Iran, Egypt, Saudi Arabia and Turkey. Even if melon (*C. melo* var. *inodorus* and *cantalupensis*), cucumber (*C. sativus*) and calabash (*Lagenaria siceraria*) are reported as possible hosts of the ladybird (Liotta, 1964), few or no data are available about the damages on these crops, as well as on zucchini (*Cucurbita pepo*) and loofah (*Luffa aegyptiaca* = *L. cylindrica*), all species economically relevant in Europe. In addition, a recent paper investigates the sensitivity of the antennae (electroantennographic EAG responses) of *C. elaterii* to VOCs emitted by Cucurbitaceae crops (*C. lanatus*, *C. melo*, *C. pepo*, *Cucurbita moschata*, *L. siceraria*, *L. aegyptiaca*, *C. sativus*), such as E2-exenal, heptanal, nonanal, decanal, methyl salicylate, linalool, Z3-hexen-1-ol, pentanol, hexanol, nonanol and octanol (Piersanti et al., 2022). Antennae of *C. elaterii* clearly respond to many of these chemicals, still data need to be available on the role of this sensory ability in host-plant selection (Piersanti et al., 2022).

In this regard, the present study aims: (i) to test the ability of female *C. elaterii* in selecting host cucurbit plants using their VOCs in a Y-tube olfactometer; (ii) to investigate the relationship between female food preferences, tested by dual-choice behavioural experiments, and larval performance, measured in terms of larval mortality, developmental time and morphometric parameters of the emerged adults. Cucurbits selected for the experiments belong to major (watermelon, melon, cucumber, zucchini, pumpkin and calabash) and minor (loofah) crops economically relevant in Europe. These species are representative of five genera widespread in the phylogenetic cladogram of Cucurbitaceae (Chomicki et al., 2019) and have been previously tested in *C. elaterii* EAG recordings (Piersanti et al., 2022).

MATERIALS AND METHODS

Insects

Adults of *C. elaterii* were collected into the field in Perugia, (Italy) (43°07′41.7″ N 12°21′43.3″ E), on plants of *Ecballium elaterium* (L.) A. Rich (Cucurbitaceae) in September 2021. Insects were kept in a culture room under controlled conditions (25 ± 2°C, 45 ± 15% RH, photoperiod LD 16:8 using lamps 3350 lm; 4000 K) inside a white net cage (30 × 30 × 30 cm) (Type 80.301, Vermandel, Hulst, the Netherlands). Insects in different developmental stages (eggs, larvae and adults) were maintained in separate cages for a maximum of 30 individuals per cage. They were fed with plants of *C. melo* var. *inodorus* (the honeydew melon, a cultivar not used in the experiments) and no free water was provided. Plants used as feed were grown in pots (as described in the next paragraph). Six plants with five healthy fully expanded leaves were provided in each cage per day. The eggs were laid on the leaf abaxial surface, and the plants with the

eggs were gently moved into a new cage. As the larvae emerged, they were carefully moved in a cage with plants; mature larvae typically pupated on the top of the larval cage and emerged adults were moved into adult cages daily. Adults of both sexes were maintained in the same cage with a sex ratio of 50% and mated females (2 weeks old) were used in the experiments. Insect sex was determined under stereomicroscope (Optika SFX-33, Ponteranica, Italy) (Dieke, 1947; Tomaszewska & Szawaryn, 2016).

Plants

Seven species of Cucurbitaceae belonging to five genera (Table 1) were grown for the experiments. The cucurbit species were selected because they are ubiquitous in Italy and represent major (watermelon, melon, cucumber, zucchini, pumpkin, calabash) and minor (loofah) cucurbit crops economically relevant (Chomicki et al., 2019). In addition, these selected species represent both annual (watermelon, melon, cucumber, zucchini, pumpkin, loofah) and perennial (calabash) crops with different phylogenetic relationships within the family Cucurbitaceae (Chomicki et al., 2019). The same species used in this study have also been used in a previous paper on the chemical ecology of *C. elaterii*, aiming to explore antennal olfactory responses to plant volatiles (Piersanti et al., 2022).

Commercial seeds (Rosi Sementi, Italy) were used to obtain plants. The seeds were sown into individual plastic pots (Bamaplast, Pistoia, Italy) (8 × 8 × 9 cm for watermelon, melon, cucumber, calabash and loofah, and 9 × 9 × 13 cm for zucchini and pumpkin, which have a larger size and more rapid growth) in sterile topsoil (Patzer Einheitserde, Manna Italia, Bolzano, Italy). Plants were grown for approximately 30 days in a controlled climate chamber (25 ± 2°C, 45 ± 15% RH, photoperiod LD 14:10) equipped with lights with a photosynthetic photon fluence rate of 200 μmol m^{-2} s^{-1} placed above the foliage. Water was supplied by sub-irrigation.

Y-tube olfactometer

The Y-tube olfactometer consisted of a polycarbonate plate (10 mm thick) (Lexan™), with a Y-shaped space milled into the centre (stem 185 mm long; arms 125 mm long at 60° angle; internal section 20 mm), sandwiched between two glass plates (10 mm thick). A 7-mm-diameter hole drilled through the polycarbonate plate into the end of each arm allowed air tube connections, and a similar hole drilled into the end of the stem permitted the airflow outlet. Compressed medical-grade air (79% nitrogen and 21% oxygen by volume), regulated by flow meters (Matheson) and humidified by bubbling through bi-distilled water (Drechsel bottle 125 mL), flowed through both arms, creating an air stream of 70 mL min^{-1} per arm. The olfactometer arena was surrounded by a cardboard screen to minimise disturbance and was illuminated by four cool white fluorescent tubes (−3350 lm; 4000 K) above the device. Temperature in the olfactometer arena was 25 ± 1.6°C.

Before entering the olfactometer arms, each air stream, controlled by flow meters, passed through a cylindrical glass chamber (Ø = 12 cm; h = 52 cm; 5.8 L) (Stereoglass S.r.l., San Martino in Campo, Italy) containing the plant responsible for odour sources. The plants used in the experiments were healthy, with five fully expanded intact leaves. The plant pot was wrapped with aluminium foil to minimise the odour from the soil. For each replicate, two plants of different species were located in the two glass chambers to produce alternative olfactory stimuli in the two arms of the olfactometer. For each bioassay, a mated female of *C. elaterii*, starved for 12 h in laboratory conditions, was introduced into the olfactometer at the entrance of the central stem. Insects were used only once to avoid any learning bias. The insect position (stem, right arm or left arm) was recorded for 5 min using EthoWatcher® (Florianópolis, Brazil). The total time spent in each arm (mean ± SE) expressed in seconds was measured and analysed. Insects that remained in the stem for 5 min were not considered in the data analysis.

Around 30 insects were tested for each pair of plant species (21 combination in total); for every 10 replicates, odour sources (plants) were replaced with new ones, and the glass chambers were washed with (in sequence) 10 mL of hexane (Sigma–Aldrich, St. Louis, MO), 10 mL of acetone (Carlo Erba, Cornaredo, Italy), 50 mL of distilled water and baked overnight (120°C). The olfactometer was cleaned and the odour sources were changed to alternate arms (to prevent any directional biases) every five replicates. The glass plates were cleaned with hexane, acetone and distilled water. In contrast, the polycarbonate part of the olfactometer was cleaned with a laboratory detergent and rinsed with hot tap water (approximately

TABLE 1 Cucurbitaceae species used in the experiments (correspondence between scientific name, variety and common name).

Species	Author	Variety	Common name
Citrullus lanatus	(Thunb) Matsumura and Nakai	var. crimson sweet	Watermelon
Cucumis melo	(L.)	var. cantalupensis	Melon
Cucumis sativus	(L.)	var. marketmore	Cucumber
Cucurbita pepo	(L.)	var. striato di Napoli	Zucchini
Cucurbita moschata	Duchesne	var. gigante gialla di Napoli	Pumpkin
Lagenaria siceraria	(Molina) Standl	var. longissima	Calabash
Luffa aegyptiaca (=L. cylindrica M. Roem)	Mill		Loofah

90°C, for 5 min) and distilled water. After washing, the polycarbonate plate was inverted. The odour sources were randomly assigned during bioassays, and the possible presence of bias was tested by running controls with both air streams passing through empty glass chambers ($n = 18$). All tests were performed between 7:00 AM and 3:00 PM (CEST), and the bioassay room was maintained at 25 ± 1.6°C, 50%–60% RH.

Dual-choice chambers

To test the existence of a feeding preference in *C. elaterii* females, insects were starved for 12 h in laboratory conditions and tested in dual-choice experiments with all possible combinations of two plant species among the seven Cucurbitaceae selected for the experiments (Table 1). In each replicate, a couple of leaves, one from each selected species, both not excised from the plant, were exposed to one mated female, caged on the surface of the two leaves using a clip cage constituting a dual-choice arena, similar to those illustrated by Piersanti et al. (2020). The clip cage consisted of a modified plastic Petri dish (9 cm diameter; 1.5 cm high) with a mesh-covered hole (6 cm diameter) and the rim covered by a small sponge ring to avoid damage to the leaf. The equal surface (around 1000 mm^2) of the two leaves was exposed to the test insect inside the clip cage. Choice tests were performed on plants with five fully expanded leaves. The insects were allowed to feed for 5 h, then the arena with the insects was removed and the leaves were photographed by a digital camera (Koppace 21MP camera 1080P, Shenzhen, China) fitted with a 12.5–75 mm/F 1.8 zoom lens. The damage due to feeding was measured from digital images using the open-source image-processing program ImageJ (Schneider et al., 2012). We considered as feeding damages brown areas or holes on the green leaves, due to the insect bites. Considering the typical leaf damage due to *C. elaterii*, it was always possible to define easily the outline of the leaf. Ten to fifteen replicates were performed for each combination of cucurbit species. All tests were made between 7:00 AM and 6:00 PM (CEST), and the bioassay room was maintained at 25 ± 1.6°C, 50%–60% RH.

Larval development

Newly hatched larvae were individually gently removed from the brood and located on an experimental host plant, where they were maintained till pupation. The plants belonged to the seven species selected for the experiments (Table 1). The single newly hatched larva was confined in a clip cage similar to those described in the dual-choice chambers bioassays. Plants used in the experiments had four to five fully expanded leaves, and the insect arena did not prevent plant growth. Larvae were checked daily; dead insects were removed and their numbers were recorded, as well as pupae. When the leaf inside the clip cage was exhausted, the insect was gently moved to a different leaf (or position) on the same plant, taking a picture of the feeding damage. The total consumed leaf area for each insect, till pupation, was measured from the sum of the consumed areas in the daily digital images, using the open-source image-processing program ImageJ (Schneider et al., 2012).

The pupated insects were moved individually in a plastic jar (30 mm diameter and 50 mm height) till emergence. When the adult emerged, as soon as the cuticle was hardened (with a darker colour), sex and biometric parameters (length of elytra and width of the pronotum) were recorded. The duration of postembryonic development (days) was calculated (ranging between 24 and 53 days). The individual development of 15–25 larvae for each host-plant species was observed. Experiments were run under controlled conditions between May and September 2021 (25 ± 2°C, 45 ± 15% RH, photoperiod LD 14:10).

Statistical analysis

In the Y-tube olfactometer tests, the time spent by *C. elaterii* in the two arms of the olfactometer was analysed by linear mixed models (LMM) with the plant species as fixed effect and insect nested within each plant pair as random effects to account for pseudoreplication (females tested towards the same plant pair). The significance of the fixed term in the model was determined using likelihood ratio tests (LRTs) comparing the model with and without the factor in question (Crawley, 2007). Because this approach compares models with different fixed-effect structures, maximum likelihood (ML) was specified in the models instead of restricted maximum likelihood (REML) (Crawley, 2007). Model fit was assessed with residual plots. The statistical analyses were carried out using the package lme4 (Bates et al., 2015) of R software, version 4.2.2 (R Core Team, 2020). In the dual-choice chambers tests, to analyse the difference in the leaf area damaged by the insects, the Wilcoxon signed-rank test was used because data were not normally distributed. The larval mortality recorded on the different plant species was compared using the Pearson Chi-square test followed by Goodman's post hoc procedure (Marascuilo & Serlin, 1988). The two-way analysis of variances, considering the plant species and the sexes as factors, was used to compare data regarding the development time, the length of elytra and width of the pronotum of the adults, and the consumed leaf area in the larval development experiments. The Tukey unequal N HSD (honestly significant difference) post hoc test was used for post hoc comparisons. Plant species were compared for males and females when the sex factor was statistically different and the interaction effect between plant and sexes was not significant. When the difference between sexes was not different only plant species were compared (Statsoft, 2001). In the larval development experiments, plants that did not allow to complete the development were not included in the analysis regarding the development duration and the adult morphometric parameters. Before the analysis, the data normality was tested with Shapiro–Wilk test and the homogeneity of variances with Cochran C test. Data regarding post embryonic development duration and leaf damage produced by

melon ladybird larvae were subjected to Box–Cox transformations to reduce heteroscedasticity (Sokal & Rohlf, 1998).

RESULTS

Y-tube olfactometer

No significant difference in the time spent by the ladybirds ($t = 0.40$; d.f. $= 17$; $p = 0.6944$) in each of the two arms in the control tests was recorded. Considering all the 21 possible combinations of the seven Cucurbitaceae used for the experiments (Figure 1 and Table 2), only five cases showed a significant difference in the time spent by the ladybirds in the two arms. In detail, insects spent more time in the arm with volatiles emitted by calabash than in the arm with volatiles emitted by pumpkin, in the arm with volatiles emitted by watermelon than in the arm with volatiles emitted by loofah, in the arm with volatiles emitted by watermelon than in the arm with volatiles emitted by pumpkin, in the arm with volatiles emitted by melon than in the arm with volatiles emitted by pumpkin, and in the arm with volatiles emitted by cucumber than in the arm with volatiles emitted by zucchini.

Dual-choice chambers

Considering all the 21 possible combinations of the 7 Cucurbitaceae used for the experiments (Figure 2 and Table 2), loofah was always significantly refused by the insects (in detail, it was never eaten, except one replicate with pumpkin and one with cucumber). Calabash elicited a very low feeding activity and was quite often significantly refused in all combinations. Insects did not eat either loofah or calabash in bioassays comparing the two plant species. Watermelon was preferred (larger surface of leaf damage) when compared with loofah, calabash, pumpkin and cucumber. Melon was preferred to loofah, calabash and watermelon. Pumpkin, zucchini and cucumber were chosen only when offered with loofah or calabash. In the remaining eight combinations, there was no significant choice by the insects; in fact, the consumed leaf areas were not significantly different.

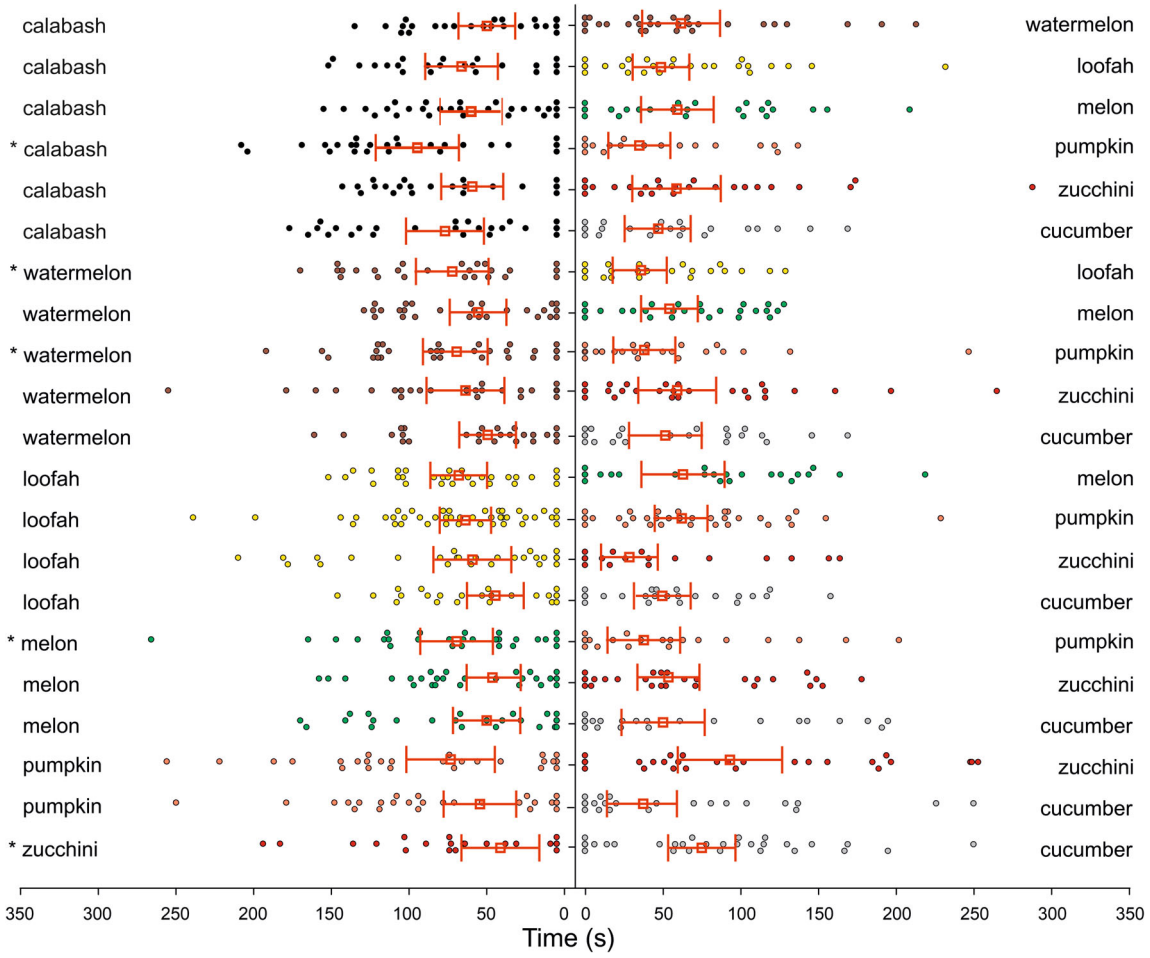


FIGURE 1 Time (s) spent by melon ladybirds in each arm of the Y-tube olfactometer during the bioassays. Strip chart with superimposed mean and 95% confidence intervals, each plant species is represented with a specific colour. Statistical parameters for each plant combination are reported in Table 2. Asterisk (*) indicates significant difference at $p < 0.05$ (linear mixed model). Each colour indicates one species of Cucurbitaceae.

TABLE 2 Statistical parameters in the analysis of the responses obtained in Y-tube olfactometer (linear mixed model, see Figure 1) and dual-choice chamber (Wilcoxon signed-rank test, see Figure 2) experiments.

Tested plants	Y-tube olfactometer	Dual-choice chamber
Calabash–watermelon	$f = 1.55$; $n = 29$; $p = 0.217$	**$Z = 2.31$, $n = 11$; $p = 0.019$**
Calabash–loofah	$f = 1.36$; $n = 30$; $p = 0.248$	**$n = 15$**
Calabash–melon	$f = 0.02$; $n = 30$; $p = 0.882$	**$Z = 3.18$; $n = 13$; $p < 0.001$**
Calabash–pumpkin	$f = 9.90$; $n = 35$; $p = 0.002$	**$Z = 2.13$; $n = 11$; $p = 0.032$**
Calabash–zucchini	$f = 0.06$; $n = 36$; $p = 0.804$	**$Z = 2.34$; $n = 13$; $p = 0.017$**
Calabash–cucumber	$f = 2.19$; $n = 36$; $p = 0.143$	**$Z = 3.06$; $n = 12$; $p < 0.001$**
Watermelon–loofah	**$f = 4.19$; $n = 29$; $p = 0.045$**	**$Z = 2.80$ $n = 10$; $p = 0.002$**
Watermelon–melon	$f = 0.13$; $n = 32$; $p = 0.722$	**$Z = 1.99$; $n = 11$; $p = 0.046$**
Watermelon–pumpkin	**$f = 4.10$; $n = 32$; $p = 0.047$**	**$Z = 1.99$; $n = 10$; $p = 0.049$**
Watermelon–zucchini	$f = 0.02$; $n = 32$; $p = 0.876$	$Z = 0.26$; $n = 10$; $p = 0.846$
Watermelon–cucumber	$f = 0.09$; $n = 30$; $p = 0.771$	**$Z = 2.80$; $n = 10$; $p = 0.002$**
Loofah–melon	$f = 0.04$; $n = 30$; $p = 0.853$	**$Z = 3.30$; $n = 14$; $p < 0.001$**
Loofah–pumpkin	$f = 0.82$; $n = 42$; $p = 0.452$	**$Z = 2.60$; $n = 10$; $p = 0.006$**
Loofah–zucchini	**$f = 3.73$; $n = 32$; $p = 0.058$**	**$Z = 2.80$; $n = 10$; $p = 0.002$**
Loofah–cucumber	$f = 0.48$; $n = 30$; $p = 0.493$	**$Z = 2.93$; $n = 11$; $p < 0.001$**
Melon–pumpkin	**$f = 4.43$; $n = 30$; $p = 0.039$**	$Z = 0.28$; $n = 14$; $p = 0.808$
Melon–zucchini	$f = 0.42$; $n = 35$; $p = 0.519$	$Z = 0.94$; $n = 12$; $p = 0.380$
Melon–cucumber	$f = 0.01$; $n = 33$; $p = 0.912$	$Z = 1.70$; $n = 15$; $p = 0.095$
Pumpkin–zucchini	$f = 0.61$; $n = 33$; $p = 0.439$	$Z = 1.69$; $n = 11$; $p = 0.102$
Pumpkin–cucumber	$f = 0.79$; $n = 38$; $p = 0.375$	$Z = 1.10$; $n = 12$; $p = 0.301$
Zucchini–cucumber	**$f = 4.65$; $n = 35$; $p = 0.034$**	$Z = 0.18$: $n = 11$; $p = 0.898$

Note: Parameters are reported for each pair of host-plants combination, proposed to *Chnootriba elaterii* females during the bioassays. Significant differences are highlighted in bold.

Larval development

The mortality (%) among larvae fed with the different plan species was significantly different ($\chi^2 = 15.68$; d.f. = 6; $p = 0.0155$), indeed no larvae completed development on loofah and all the insects tested died in a few days (Figure 3). In the other cucurbits, only 20%–30% of larvae died during the experiments, without significant differences between the plant species ($\chi^2 = 15.68$; d.f. = 6; $p = 0.0155$) (Figure 3). The remaining larvae completed the development and reached the adult stage in less than 55 days. The insect's development time was different on the different plant species and between the two sexes, but the interaction of the two factors was not different. In particular, the development was slightly longer on melon (up to 50 days for some males) and shorter on watermelon (less than 30 days for all insects) (Plant species: $F = 1.6$; d.f. = 5, 65; $p < 0.0001$, Sex: $F = 8.30$; d.f. = 1, 65; $p = 0.0054$, Plant species × sex: $F = 2.19$; d.f. = 5, 65; $p = 0.0660$) (Figure 4).

The length of elytra (Plant species: $F = 1.76$; d.f. = 5, 60; $p = 0.1367$, Sex: $F = 6.43$; d.f. = 1, 60; $p = 0.0138$, Plant species × sex: $F = 1.79$; d.f. = 5, 60; $p = 0.1295$), and the width of the pronotum (Plant species: $F = 0.88$; d.f. = 5, 56; $p = 0.5013$, Sex: $F = 7.72$; d.f. = 1, 56; $p = 0.0074$, Plant species × sex: $F = 0.70$; d.f. = 5, 56; $p = 0.6289$) of adults obtained from larvae developed on the six cucurbit species were not different and no differences were also found for these parameters between the two sexes and in the interaction of the two factors. Loofah was not included because it did not allow to obtain any adult (Figure 5). The leaf damage was different among the plant species (F = 49.7; d.f. = 6, 77; p < 0.0001) but not between the two sexes (Sex: F = 0; d.f. = 1, 77; p = 0.9648) and their interaction (Plant species × sex: F = 0.7; d.f. = 6, 77; p = 0.6599) (Figure 6). Larvae never ate loofah, then the leaf damage was zero. In the remaining cucurbits, the leaf damaged area was reduced in the watermelon and melon leaves compared with zucchini. The other cucurbits showed an intermediate leaf damage (Figure 6).

DISCUSSION

Olfaction in phytophagous insects is one of the major drivers used to detect the host-plant in the environment, both in long (Bernays & Chapman, 1994; Carrasco et al., 2015) and in short distance (Vaishampayan et al., 1975).

Notwithstanding many authors demonstrating the crucial role of olfaction in phytophagous Coleoptera (Jackson et al., 2005; Lewis et al., 1990; Rondoni et al., 2017; Stenberg & Ericson, 2007), and despite a significative selective response of *C. elaterii* females in 5 of

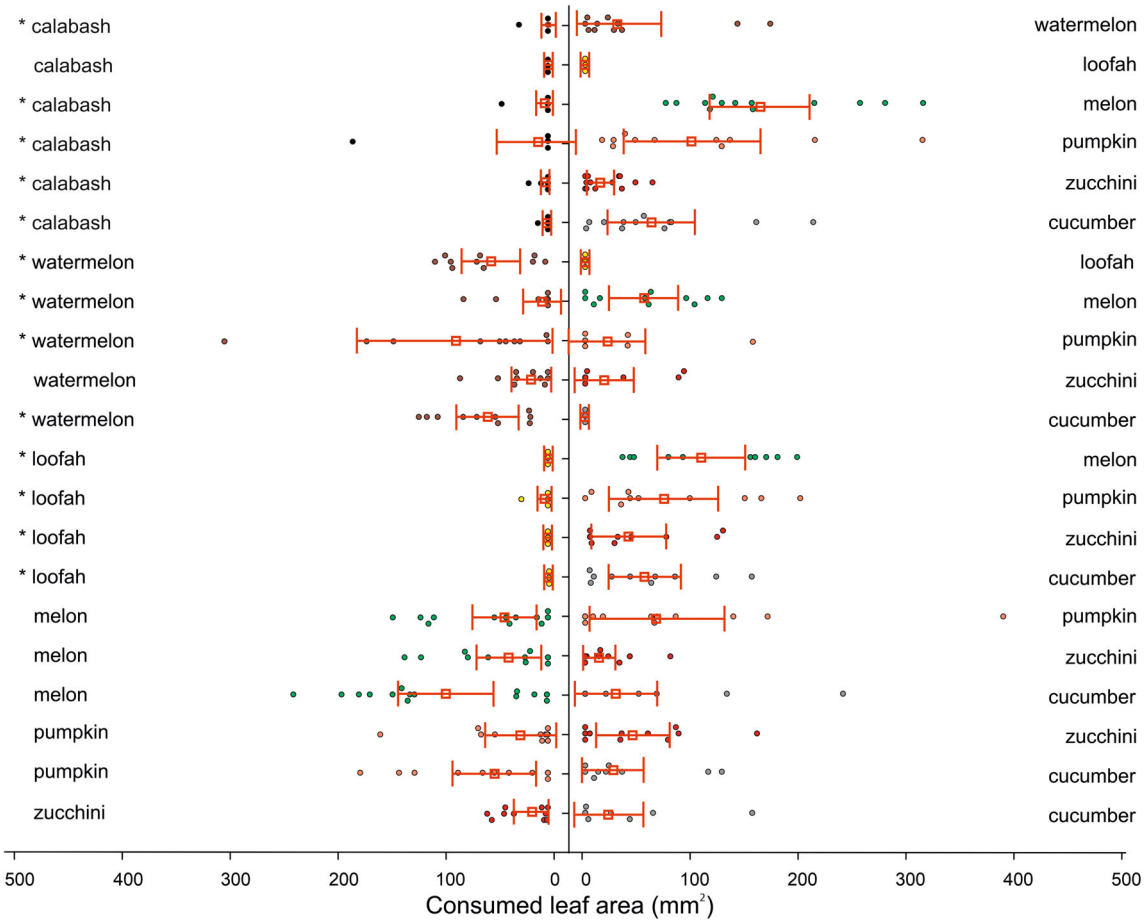


FIGURE 2 Consumed leaf area (mm^2) produced by feeding of female melon ladybirds in the dual-choice chamber experiments. Strip chart with superimposed mean and 95% confidence intervals, each plant species is represented with a specific colour. Statistical parameters are reported in Table 2. Asterisk (*) indicates significant difference at $p < 0.05$ (Wilcoxon signed-rank test). Each colour indicates one species of Cucurbitaceae.

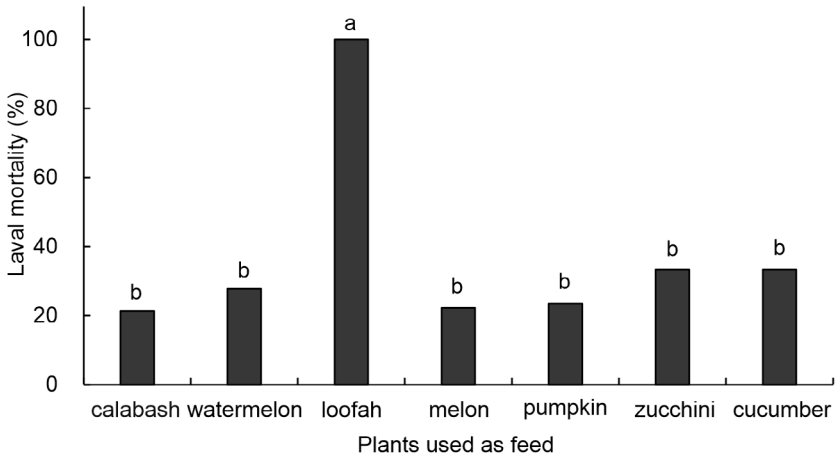


FIGURE 3 Larval mortality (total %) on the cucurbit species used as a host plant in developmental experiments. Columns with different letters are significantly different at $p < 0.05$ (Pearson χ^2, Goodman's post hoc procedure).

the 21 proposed combinations of plants in the Y-tube olfactometer bioassays, our results suggest that in this species the olfactory cues alone only partially may have a role in identifying host plants. Indeed, melon ladybird females in Y-tube olfactometer (i) did not refuse loofah and calabash, clearly rejected in the dual-choice tests; (ii) showed a significant preference for volatiles emitted by melon and watermelon

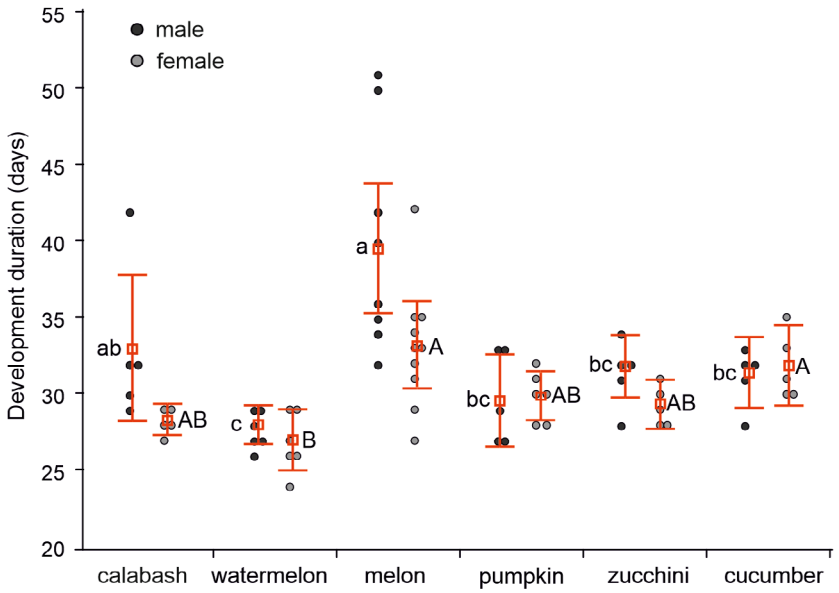


FIGURE 4 After embryonic development duration (days), from neo hatched larva to the adult, on the cucurbit species used as host plants for developmental experiments. Strip chart with superimposed mean and 95% confidence intervals. Strips with different letters are significantly different at $p < 0.05$ (two-way analysis of variance, Tukey unequal N honestly significant difference); upper case letters are used for female and lower case letters are used for males.

(preferred host in dual-choice experiments) only when proposed in comparison with pumpkin; (iii) preferred calabash to pumpkin, notwithstanding the first one was largely refused in the dual-choice feeding tests.

These results were not expected given previous EAG investigations, demonstrating that antennae of *C. elaterii* can perceive a wide range of volatiles emitted by cucurbits (E2-exenal, heptanal, nonanal, decanal, methyl salicylate, (-) -linalool, Z3-hexen-1-ol, pentanol, hexanol, nonanol and octanol), and plant extracts from watermelon, melon, pumpkin, calabash, cucumber and zucchini but not loofah (Piersanti et al., 2022). We cannot exclude that olfactory cues may be important in host searching by melon ladybug, but probably in combination with other stimuli, as reported in many insects orders (Fernandez & Hilker, 2007; Harris & Miller, 1988; Prokopy & Owens, 1978; Saxena & Goyal, 1978; Vaishampayan et al., 1975). Similar results were found by Stenberg and Ericson (2007) also in *Altica engstroemi* (Sahlberg) (Coleoptera: Chrysomelidae), a monophagous chrysomelid that was guided to its host plant by visual and olfactory cues, but never responded to plant VOCs in Y-tube olfactometer. Very little is known about how olfactory cues interact with other stimuli in the central nervous system of herbivorous insects; still, undoubtedly, multimodal signals provide a degree of redundancy that can be advantageous in complex environments (Carrasco et al., 2015). In addition, unlike monophagous insects that can rely on specific volatiles to locate their best host plant, females of oligophagous insects may have high phenotypic plasticity and use multiple cues integration because there can be no common infochemicals indicative of plant quality in a range of host plants (Carrasco et al., 2015). Furthermore, the search for new habitats, unlike in other insects (Ferracini et al., 2023; Toepfer et al., 2006), is probably not a recurrent activity for *C. elaterii* whose adults are weak flyers with a limited dispersal ability (Liotta, 1964). Based on the present results, loofah cannot be considered as host plant for *C. elaterii*; indeed, adult females do not feed on its leaves, and larvae do not develop on them. This is in agreement with EAG investigation (Piersanti et al., 2022), where loofah extract did not elicit any antennal response of adults. This plant is widely distributed in Africa and Asia, and fruits, traditionally used as sponges (Chomicki et al., 2019), are recently considered a promising sustainable and renewable biomass for new materials development (Hlel et al., 2021; Paglicawan et al., 2005; Su et al., 2018). The unpalatability of loofah could be due to some chemical defence, as suggested by the absence of EAG responses to loofah extract (Piersanti et al., 2022), which aligns with previous preliminary observations (El-Abdin & Siragelnour, 1991); otherwise, *C. elaterii* does not have any problem of adhesion to the loofah leaves (Saitta et al., 2022). For this reason, loofah could be used as an intercrop in cucurbit cultivations, developing interesting biocontrol strategies against the melon ladybug, similar to the protection of cabbage crops from *Pieris rapae* (L.) (Lepidoptera: Pieridae) using tomato, fennel and catnip (Wu et al., 2010).

Despite the uncertain role of olfaction in discriminating between cucurbits, female ladybirds show clear food preferences: watermelon is the most selected food in dual-choice chambers, where it was preferred in all the proposed combination, except those with zucchini and melon. Melon, at the same time, was preferred to watermelon, while calabash and loofah were firmly refused in all the combinations, and loofah was sampled by only 2 insects out of 70. Adult females regularly feed zucchini, pumpkin and cucumber but did not prefer them to other cucurbits, except loofah and calabash. These results agree with previous reports (Akandeh & Shishehbor, 2011; Awadalla et al., 2011; Wool & van Emden, 1981), where the watermelon was the preferred food, just after the snake cucumber (*C. melo* var. *flexuosus*).

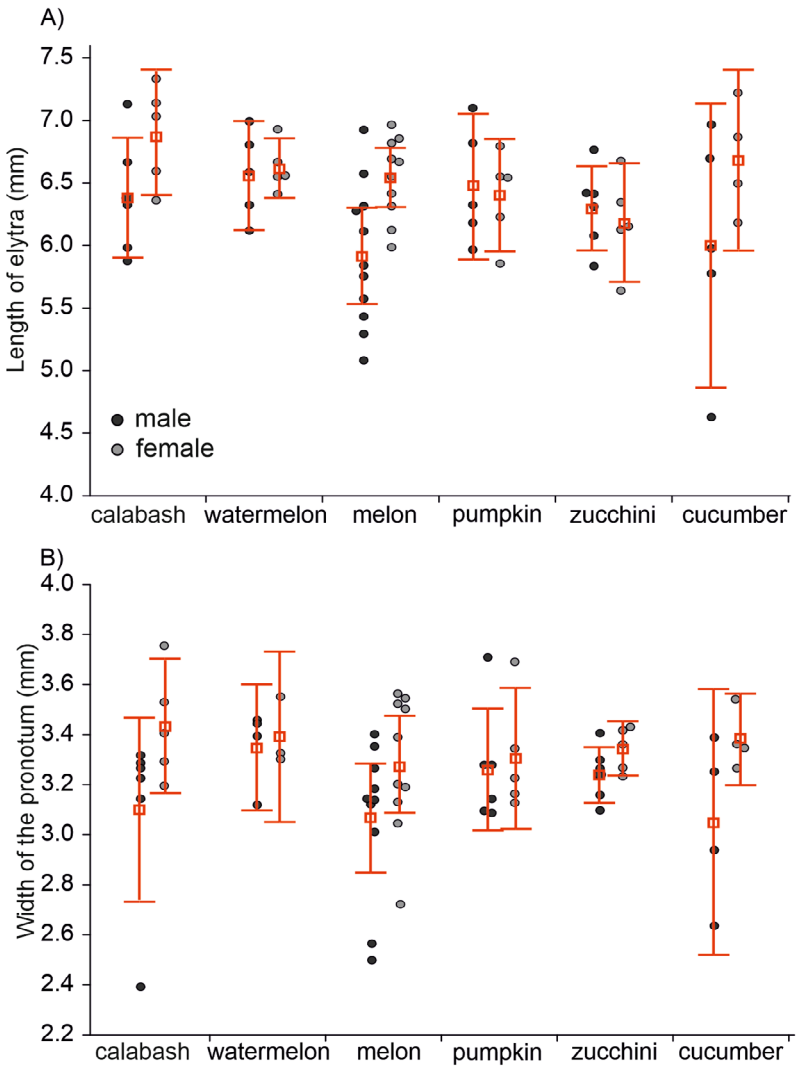


FIGURE 5 Morphometric parameters of the emerged adults grown on the different cucurbit species used as host plants for developmental experiments: (a) length of elytra (mm) and (b) width of the pronotum (mm). Strip chart with superimposed mean and 95% confidence intervals. Among plant species, no significant differences are reported at $p < 0.05$ (two-way analysis of variances).

Our experiments did not test snake cucumber but the conspecific melon (*C. melo* var. *cantalupensis*), because it is a major European crop of a different variety. On this account, it is unsurprising that varieties of the same species result in different palatability and nutritional quality due to domestication and selection (Bayhan & Bayhyan, 2017; Chomicki et al., 2019). For example, in laboratory experiments with watermelon, the crimson tide cultivar was preferred by *C. elaterii* and guaranteed the shortest development time (Bayhan & Bayhyan, 2017).

In many phytophagous insects, particularly those with low larval mobility, such as *C. elaterii* (Agrò et al., 2011; Liotta, 1964), host-plant selection is commonly assumed to depend on ovipositing females (Berdegué et al., 1998). In this context, one would intuitively expect a positive correlation between adult preferences and offspring developmental performances (Gripenberg et al., 2010; Pappers et al., 2002). This correlation is tighter for specialist insects than for generalist (Jones & Agrawal, 2019) and it is the main basic assumption of the preference-performance hypothesis (Menacer et al., 2021). This assumption is not always true (Carrasco et al., 2015; Gripenberg et al., 2010; Mayhew, 2001; Pappers et al., 2002; Thompson, 1988), as reported in *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae), whose females prefer *Chenopodium murale* L. (Caryophyllales: Amaranthaceae) while larvae show better performance on *Apium graveolens* L. (Apiales: Apiaceae) (Berdegué et al., 1998). In our experiments, no relevant differences were noticed in larval mortality and morphometric parameters of the emerged adults comparing the host plants, except loofah where larvae never developed. Considering the developmental duration, larvae grew faster on watermelon, compared with other tested plants. Shorter development duration guarantee an earlier emersion of adults, then, probably, a reproductive advantage and a larger capacity for population increase (Nylin, 2001). For this reason, this parameter is considered a useful trait to characterise larval performance (Berdegué et al., 1998; Menacer et al., 2021). Watermelon is also one of the favourite foods for adult females that, similar to other herbivore species, could perform host selection

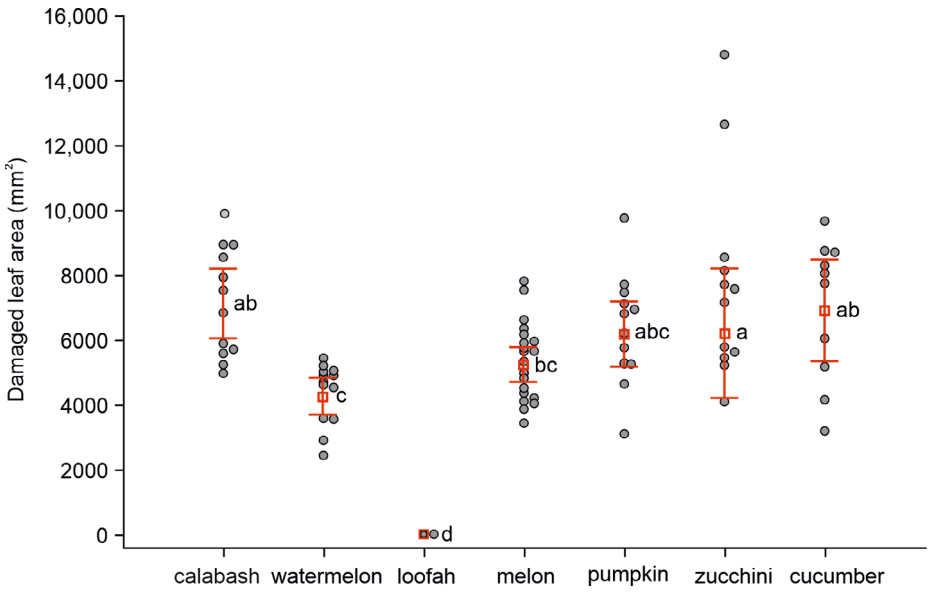


FIGURE 6 Consumed leaf area (mm^2) produced by melon ladybird larvae feeding on the cucurbits proposed as host plants during the developmental experiments. Strip chart with superimposed mean and 95% confidence intervals. Strips with different letters are significantly different at $p < 0.05$ (two-way analysis of variances, Tukey unequal N honestly significant difference). Larvae never eat loofah.

considering their food preferences (Mayhew, 2001). The adult preference for melon over watermelon, not related to better larval performance, could allow a direct advantage for the female, in terms of best survival or fecundity (Mayhew, 2001), all aspects that need to be better explored. Still, melon ladybird larvae regularly developed also on calabash, whose leaves were firmly refused by adults. This divergence may be due to plant mechanical defences. Indeed, the adhesion of insects to plant surfaces was largely studied (Gorb & Gorb, 2009; Prüm et al., 2012; Rebora et al., 2020a, 2020b; Salerno et al., 2018, 2020, 2022; Voigt et al., 2008) and a recent paper highlighted the difficult adhesion of adult *C. elaterii* on calabash, because of a dense layer of short and flexible trichomes creating a velvet surface (Saitta et al., 2022). Larvae caged in our developmental experiments, unlike adults, could not move away from velvet leaves, and then regularly feed on them.

Insects are able to regulate nutrient intake when they are in the presence of imbalanced food sources; for example, studies carried out on grasshoppers show that they are capable of applying a compensatory feeding among poor and rich food sources (Berner et al., 2005). Likewise, lower feeding damages performed by larvae on watermelon could be due to the higher nutritional quality of this plant; this agrees with adult preference in the dual-choice chamber and larval performance in terms of development duration.

CONCLUSIONS

In summary, food preference by melon ladybird females agrees with larval performance, considering the favourite crop of this pest, watermelon, and the non-host cucurbit, loofah, not allowing larval development. The lack of concordance between preference and performance concerning calabash, rejected by adults but able to guarantee normal larval development, is probably explained by the mechanical defences of the plant. The adult preference for melon over watermelon, not related to a better larval performance, can be considered maladaptive or the expression of an alternative adaptive strategy. It also suggests that the preference-performance of this insect is complex and needs further studies to be clarified. In addition, results obtained in Y-tube olfactometer show that olfaction alone probably is not sufficient to drive *C. elaterii* in host-finding process, or at least that this ability is context-dependent, based on the host combination.

To our knowledge, there are no data relating adult food preferences with larval performance in Epilachnini, or investigating the role of olfaction in host-plant selection from a behavioural perspective in melon ladybird. Elucidating the role of chemical cues in insect–plant interaction is crucial to developing effective and successful integrated pest management strategies, such as the push and pull crop and intercrop strategies (Khan et al., 2008), or the use of trap crops in collard (Piersanti et al., 2020). For example, our results suggest that loofah could be a promising 'push' species, to protect cucurbits crops from *C. elaterii*. This perspective could be interesting because several insecticides are recommended to control oligophagous pests; still, most of them are unsuitable or with low efficacy, owing to the emergence of resistant strains and toxicity to human and non-target organisms (Abdel-Moniem et al., 2004). In this context, the present results could significantly enhance the control of *C. elaterii* in organic cucurbit crops and introduce further studies to deepen the knowledge of the complex preference performance of these insects.

AUTHOR CONTRIBUTIONS

Valerio Saitta: Data curation; conceptualization; methodology; writing – review and editing; investigation. **Silvana Piersanti:** Writing – original draft; investigation; conceptualization; methodology;

data curation; writing – review and editing. **Manuela Rebora:** Data curation; conceptualization; methodology; writing – review and editing. **Gianandrea Salerno:** Data curation; conceptualization; methodology; writing – review and editing; supervision; formal analysis; visualization.

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CONFLICT OF INTEREST STATEMENT

The authors have no relevant financial or non-financial interests to disclose.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ETHICS STATEMENT

This study did not require any ethic approval.

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REFERENCES

Abdel-Moniem, A.S.H., Gomaa, A.A., Dimetry, N.Z., Wetzel, T. & Volkmar, C. (2004) Laboratory evaluation of certain natural compounds against the melon ladybird beetle, *Epilachna chrysomelina* F. attacking cucurbit plants. *Archives of Phytopathology and Plant Protection*, 37(2), 71–81. Available from: https://doi.org/10.1080/03235400410001662616

Agrò, A., Cusumano, A., Lo Genco, A. & Lo Pinto, M. (2011) Indagine su *Henosepilachna elaterii* (Rossi) (=*Epilachna chrysomelina* (F.)) e *Raphidopalpa foveicollis* (Lucas) in meloneti biologici della Sicilia occidentale. In: Regione Siciliana (Ed.) *Progetto per Lo Sviluppo Dell'agricoltura Biologica in Sicilia*, Palermo: Qanat Edizioni, pp. 175–182.

Akandeh, M. & Shishehbor, P. (2011) Life history traits of melon ladybeetle, *Epilachna chrysomelina* (Col.: Coccinellidae), on four host plant species. *Journal of Entomological Society of Iran*, 31(1), 17–27.

Akandeh, M., Shishehbor, P., Mosadegh, M.S. & Khajezadeh, Y. (2011) Sampling program and host preference of melon ladybeetle, *Epilachna chrysomelina* (F.) on some hosts of cucurbit family in Ahvaz, Southwest Iran. *Iranian Journal of Plant Protection Science*, 42(1), 1–10.

Al-Digail, S.A., Assagaf, A.I. & Mahyoub, J.A. (2012) Effect of temperature and humidity on the population abundance of spotted oriental cucumber beetle *Epilachna chrysomelina* (F.) (Coccinellidae: Coleoptera) In Al – Qunfudah Western Saudi Arabia. *Current World Environment: An International Research Journal of Environmental Sciences*, 7(1)s, 7–12. Available from: https://doi.org/10.12944/cwe.7.1.02

Ali, M.A. & Saeady, A.A.I. (1980) *Influence of temperature, photoperiod, and host-plant on the bionomics of the melon ladybird Epilachna crysomelina*. In Proocedings of the fourth conferencess on the biological aspects of Saudi Arabia. Available from: https://www.cabdirect.org/cabdirect/abstract/19812609621 [Accessed 20-08-2022].

Awadalla, S., Abd-Wahab, H., Abd El-Baky, N. & Abdel-salam, S. (2011) Host plant preference of the melon ladybird beetle *Epilachna chrysomelina* (F.) (Coleoptera: Coccinellidae) on different cucurbit vegetables in Mansoura Region. *Journal of Plant Protection and Pathology*, 2(1), 41–47. Available from: https://doi.org/10.21608/jppp.2011.84653

Awmack, C. & Leather, S. (2002) Host plant quality and fecundity in herbivorous insects. *Annual Review of Entomology*, 47(1), 817–861. Available from: https://doi.org/10.1146/annurev.ento.47.091201.1.145300

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67, 1–48. Available from: https://doi.org/10.48550/arXiv.1406.5823

Bayhan, E. & Bayhyan, S.Ö. (2017) Determination of some biological parameters *Henosepilachna elaterii* Rossi (Coleoptera: Coccinellidae) on different watermelon cultivars. *Middle East Journal of Science*, 3(1), 1–8. Available from: https://doi.org/10.23884/mejs.2017.3.1.010

Berdegué, M., Reitz, S.R. & Trumble, J.T. (1998) Host plant selection and development in *Spodoptera exigua*: do mother and offspring know best? *Entomologia Experimentalis et Applicata*, 89(1), 57–64. Available from: https://doi.org/10.1046/J.1570-7458.1998.00381.X

Bernays, E. & Chapman, R. (1994) *Host-plant selection by phytophagous insects*, Vol. 2. New York: Chapman and Hall. 312.

Berner, D., Blanckenhorn, W.U. & Körner, C. (2005) Grasshoppers cope with low host plant quality by compensatory feeding and food selection: N limitation challenged. *Oikos*, 111(3), 525–533. Available from: https://doi.org/10.1111/j.1600-0706.2005.14144.x

Beyene, Y., Hofsvang, T. & Azerefegne, F. (2007) Population dynamics of tef *Epilachna* (Chnootriba similis Thunberg)(Coleoptera, Coccinellidae) in Ethiopia. *Crop Protection*, 26(11), 1634–1643. Available from: https://doi.org/10.1016/j.cropro.2007.01.005

Carrasco, D., Larsson, M. & Anderson, P. (2015) Insect host plant selection in complex environments. *Current Opinion in Insect Science*, 8, 1–7. Available from: https://doi.org/10.1016/j.cois.2007.01.014

Chomicki, G., Schaefer, H. & Renner, S.S. (2019) Origin and domestication of Cucurbitaceae crops: insights from phylogenies, genomics and archaeology. *New Phytologist*, 226(5), 1240–1255. Available from: https://doi.org/10.1111/nph.16015

Crawley, M.J. (2007) *The R book. Chichester England: John Wiley & Sons*, Wiley Ltd 876, pp. 879.

Dieke, G. (1947) Ladybeetles of the genus Epilachna (sens. lat.) in Asia, Europe, and Australia. *Smithsonian miscellaneous. Collections*, 106, 1-180.

El-Abdin, A.M.Z. & Siragelnour, B.G. (1991) Biological aspects, food preference and chemical control of the cucurbit beetle, *Henosepilachna elaterii* (Rossi) (Coleoptera; Coccinellidae). *Arab Journal of Plant Protection*, 9(2), 103–110.

Fernandez, P. & Hilker, M. (2007) Host plant location by Chrysomelidae. *Basic and Applied Ecology*, 8(2), 97–116. Available from: https://doi.org/10.1016/j.baae.2006.05.001

Ferracini, C., Saitta, V., Rondoni, G. & Rollet, I. (2023) Variables affecting the pine processionary moth flight: a survey in the North-Western Italian Alps. *Forests*, 14(1), 31. Available from: https://doi.org/10.3390/F14010031

Gorb, E. & Gorb, S. (2009) Effects of surface topography and chemistry of *Rumex obtusifolius* leaves on the attachment of the beetle *Gastrophysa viridula*. *Entomologia Experimentalis et Applicata*, 130(3), 222–228. Available from: https://doi.org/10.1111/j.1570-7458.2008.00806.x

Gripenberg, S., Mayhew, P., Parnell, M. & Roslin, T. (2010) A meta-analysis of preference–performance relationships in phytophagous insects. *Ecology Letters*, 13(3), 383–393. Available from: https://doi.org/10.1111/j.1461-0248.2009.01433.x

Hansson, B. & Stensmyr, M. (2011) Evolution of insect olfaction. *Neuron*, 72(5), 698–711. Available from: https://doi.org/10.1016/j.neuron.2011.11.003

Harris, M. & Miller, J. (1988) Host-acceptance behaviour in an herbivorous fly, *Delia antiqua*. *Journal of Insect Physiology*, 34(3), 179–190. Available from: https://doi.org/10.1016/0022-1910(88)90048-0

Hlel, T., Belhadj, F., Gül, F., Altun, M., Yağlıoğlu, A., Smaali, I. et al. (2021) The molecular characterization and biological assessment of the leaves extracts of loofah reveal their nutraceutical potential. *Recent Patents on Food, Nutrition & Agriculture*, 12(1), 63–72. Available from: https://doi.org/10.2174/2212798411999201110211931

Hufnagel, M., Schilmiller, A.L., Ali, J. & Szendrei, Z. (2017) Choosy mothers pick challenging plants: maternal preference and larval performance of a specialist herbivore are not linked. *Ecological Entomology*, 42(1), 33–41. Available from: https://doi.org/10.1111/EEN.12350

Jackson, D., Sorensen, K., Sorensen, C. & Story, R. (2005) Monitoring cucumber beetles in sweetpotato and cucurbits with kairomone-baited traps. *Journal of Economic Entomology*, 98(1), 159–170. Available from: https://doi.org/10.1603/0022-0493-98.1.159

Jaenike, J. (1978) On optimal oviposition behavior in phytophagous insects. *Theoretical Population Biology*, 14(3), 350–356. Available from: https://doi.org/10.1016/0040-5809(78)90012-6

Jones, P.L. & Agrawal, A.A. (2019) Beyond preference and performance: host plant selection by monarch butterflies, *Danaus plexippus*. *Oikos*, 128(8), 1092–1102. Available from: https://doi.org/10.1111/OIK.06001

Khan, Z., Midega, C., Amudavi, D., Hassanali, A. & Pickett, J. (2008) On-farm evaluation of the 'push–pull' technology for the control of stemborers and striga weed on maize in western Kenya. *Field Crops Research*, 106(3), 224–233. Available from: https://doi.org/10.1016/j.fcr.2007.12.002

Lewis, P., Lampman, R. & Metcalf, R. (1990) Kairomonal attractants for *Acalymma vittatum* (Coleoptera: Chrysomelidae). *Environmental Entomology*, 19(1), 8–14. Available from: https://doi.org/10.1093/ee/19.1.8

Liotta, G. (1964) Contributo alla conoscenza della biologia dell'*Epilachna chrysomelina* F. Sicilia (Col. Coccinellidae). *Bollettino Idell'istituto di Entomologia Agraria e dell'Osservatorio di Fitopatologia di Palermo*, 5, 235-262.

Marascuilo, L. & Serlin, R. (1988) *Statistical methods for the social and behavioral sciences*. New York, WH Freeman & Co.

Mayhew, P.J. (2001) Herbivore host choice and optimal bad motherhood. *Trends in Ecology & Evolution*, 16(4), 165–167. Available from: https://doi.org/10.1016/S0169-5347(00)02099-1

Menacer, K., Cortesero, A.M. & Hervé, M.R. (2021) Challenging the preference–performance hypothesis in an above-belowground insect. *Oecologia*, 197(1), 179–187. Available from: https://doi.org/10.1007/S00442-021-05007-5

Nardi, C., Rech, C., Oliveira, J.R.F., Peñaflor, M.F.G.V., Santos, F. & Bento, J.M.S. (2023) Preference-performance hypothesis and host oviposition selection of *Diabrotica speciosa*: aboveground female avoids belowground conspecific larvae in maize. *Arthropod-Plant Interactions*, 17, 1–10. Available from: https://doi.org/10.1007/S11829-023-09972-X

Nylin, S. (2001) Life history perspectives on pest insects: what's the use? *Austral Ecology*, 26(5), 507–517. Available from: https://doi.org/10.1046/j.1442-9993.2001.01134.x

Paglicawan, M.A., Cabillon, M.S., Cerbito, R.P. & Santos, E.O. (2005) Loofah fiber as reinforcement material for composite. *The Philippine Journal of Science*, 134(2), 113–120.

Pappers, S., Van der Velde, G. & Ouborg, J. (2002) Host preference and larval performance suggest host race formation in *Galerucella nymphaeae*. *Oecologia*, 130(3), 433–440. Available from: https://doi.org/10.1007/s00442-001-0822-3

Park, H. & Yoon, I. (1991) A taxonomic revision of subfamily Epilachninae in Korea (Coleoptera: Coccinellidae). *Entomological Research Bulletin*, 17, 81–92.

Piersanti, S., Rebora, M., Ederli, L., Pasqualini, S. & Salerno, G. (2020) Role of chemical cues in cabbage stink bug host plant selection. *Journal of Insect Physiology*, 120, 103994. Available from: https://doi.org/10.1016/J.JINSPHYS.2019.103994

Piersanti, S., Saitta, V., Rebora, M. & Salerno, G. (2022) Olfaction in phytophagous ladybird beetles: antennal sensilla and sensitivity to volatiles from host plants in *Chnootriba elaterii* (Coleoptera Coccinellidae). *Arthropod-Plant Interactions*, 16, 617–630. Available from: https://doi.org/10.1007/s11829-022-09923-y

Prokopy, R. & Owens, E. (1978) Visual generalist with visual specialist phytophagous insects: host selection behaviour and application to management. *Entomologia Experimentalis et Applicata*, 24(3), 609–620. Available from: https://doi.org/10.1111/j.1570-7458.1978.tb02824.x

Prüm, B., Seidel, R. & Bohn, H. (2012) Plant surfaces with cuticular folds are slippery for beetles. *Journal of the Royal Society Interface*, 9(66), 127–135. Available from: https://doi.org/10.1098/rsif.2011.0202

R Core Team. (2020) *R: a language and environment for statistical computing. R Foundation for Statistical Computing*. Available form: https://www.r-project.org/ [Accessed 10-06-2022].

Rebora, M., Salerno, G., Piersanti, S., Gorb, E. & Gorb, S. (2020a) Role of fruit epicuticular waxes in preventing *Bactrocera oleae* (Diptera: Tephritidae) attachment in different cultivars of *Olea europaea*. *Insects*, 11(3), 189. Available from: https://doi.org/10.3390/insects11030189

Rebora, M., Salerno, G., Piersanti, S., Gorb, E. & Gorb, S. (2020b) Entrapment of *Bradysia paupera* (Diptera: Sciaridae) by *Phaseolus vulgaris* (Fabaceae) plant leaf. *Arthropod-Plant Interactions*, 14(4), 499–509. Available from: https://doi.org/10.1007/S11829-020-09760-X

Rondoni, G., Ielo, F., Ricci, C. & Conti, E. (2017) Behavioural and physiological responses to prey-related cues reflect higher competitiveness of invasive vs. native ladybirds. *Scientific Reports*, 7(1), 3716. Available from: https://doi.org/10.1038/s41598-017-03471-9

Rondoni, G., Roman, A., Meslin, C., Montagné, N., Conti, E. & Jacquin-Joly, E. (2021) Antennal transcriptome analysis and identification of candidate chemosensory genes of the Harlequin Ladybird Beetle, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae). *Insects*, 12(3), 209. Available from: https://doi.org/10.3390/insects12030209

Saitta, V., Rebora, M., Piersanti, S., Gorb, E. & Gorb, S. (2022) Effect of leaf trichomes in different species of Cucurbitaceae on attachment ability of the melon ladybird beetle *Chnootriba elaterii*. *Insects*, 13(12), 1123. Available from: https://doi.org/10.3390/insects13121123

Salerno, G., Rebora, M., Gorb, E. & Gorb, S. (2018) Attachment ability of the polyphagous bug Nezara viridula (Heteroptera: Pentatomidae) to different host plant surfaces. *Scientific Reports*, 8(1), 1–14. Available from: https://doi.org/10.1038/s41598-018-29175-2

Salerno, G., Rebora, M., Kovalev, A., Gorb, E. & Gorb, S.N. (2020) Kaolin nano-powder effect on insect attachment ability. *Journal of Pest Science*, 93(1), 315–327. Available from: https://doi.org/10.1007/s10340-019-01151-3

Salerno, G., Rebora, M., Piersanti, S., Saitta, V., Gorb, E. & Gorb, S. (2022) Coleoptera claws and trichome interlocking. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 209, 299–312. Available from: https://doi.org/10.1007/S00359-022-01554-1

Saxena, K.N. & Goyal, S. (1978) Host-plant relations of the citrus butterfly *Papilio demoleus* L.: orientational and ovipositional responses. *Entomologia Experimentalis et Applicata*, 24(1), 1–10. Available from: https://doi.org/10.1111/J.1570-7458.1978.TB02750.X

Scheirs, J., Bruyn, L. & Verhangen, R. (2000) Optimization of adult performance determines host choice in a grass miner. *Proceedings of the Royal Society of London Series B: Biological Sciences*, 267(1457),

2065–2069. Available from: https://doi.org/10.1098/rspb.2000.1250

Schneider, C.A., Rasband, W.S. & Eliceiri, K.W. (2012) NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, 9(7), 671–675. Available from: https://doi.org/10.1002/mrd.22489

Sevarika, M., Rondoni, G., Conti, E. & Romani, R. (2020) Antennal sensory organs and glands of the harlequin ladybird, *Harmonia axyridis*. *Entomologia Experimentalis et Applicata*, 169(1), 111–124. Available from: https://doi.org/10.1111/eea.12948

Sokal, R.R. & Rohlf, F.J. (1998) *Biometry: the principles and practice of statistics in biological research*. New York: Freeman W.H..

Städler, E., Hilker, M. & Meiners, T. (2002) Plant chemical cues important for egg deposition by herbivorous insects. In: M. Hilker, T. Meiners (Eds.) *Chemoecology of insect eggs and egg deposition*, Oxford: Blackwell, pp. 171–204.

Statsoft, I.N.C. (2001) *Statistica (data analysis software system)*. (No. 6), pp. 91–94.

Stenberg, J. & Ericson, L. (2007) Visual cues override olfactory cues in the host-finding process of the monophagous leaf beetle *Altica engstroemi*. *Entomologia Experimentalis et Applicata*, 125(1), 81–88. Available from: https://doi.org/10.1111/j.1570-7458.2007.00597.x

Su, X., Chen, J., Zheng, G., Yang, J., Guan, X., Liu, P. et al. (2018) Three-dimensional porous activated carbon derived from loofah sponge biomass for supercapacitor applications. *Applied Surface Science*, 436, 327–336. Available from: https://doi.org/10.1016/j.apsusc.2017.11.249

Thompson, J.N. (1988) Coevolution and alternative hypotheses on insect/plant interactions. *Ecology*, 69(4), 893–895. Available from: https://doi.org/10.2307/1941238

Toepfer, S., Levay, N. & Kissd, J. (2006) Adult movements of newly introduced alien *Diabrotica virgifera virgifera* (Coleoptera: Chrysomelidae) from non-host habitats. *Bulletin of Entomological Research*, 96(4), 327–335. Available from: https://doi.org/10.1079/BER2006430

Tomaszewska, W. & Szawaryn, K. (2016) Epilachnini (Coleoptera: Coccinellidae) – a revision of the world genera. *Journal of Insect Science*, 16(1), 101. Available from: https://doi.org/10.1093/jisesa/iew082

Vaishampayan, S.M., Waldbauer, G.P. & Kogan, M. (1975) Visual and olfactory responses in orientation to plants by the greenhouse whitefly, *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae). *Entomologia Experimentalis et Applicata*, 18(4), 412–422. Available from: https://doi.org/10.1111/J.1570-7458.1975.TB00418.X

Valladares, G. & Lawton, J. (1991) Host-plant selection in the holly leaf-miner: does mother know best? *The Journal of Animal Ecology*, 60, 227–240. Available from: https://doi.org/10.2307/5456

Voigt, D., Schuppert, J., Dattinger, S. & Gorb, S. (2008) Sexual dimorphism in the attachment ability of the Colorado potato beetle *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae) to rough substrates. *Journal of Insect Physiology*, 54(5), 765–776. Available from: https://doi.org/10.1016/j.jinsphys.2008.02.006

Wang, Y., Li, R., Wang, X., Liu, X. & Chen, F. (2022) Elevated CO_2 altered rice VOCs aggravate population occurrence of brown planthoppers by improving host selection ability. *Biology*, 11(6), 882. Available from: https://doi.org/10.3390/biology11060882

Wool, D. & van Emden, H.F. (1981) Influence of temperature, photoperiod and host-plant on the bionomics of the melon ladybird *Epilachna chrysomelina* (F.) (Coleoptera: Coccinellidae). *Zeitschrift für Angewandte Entomologie*, 91(1–5), 256–262. Available from: https://doi.org/10.1111/j.1439-0418.1981.tb04477.x

Wu, L., Lu, W., Yuan, G., Xu, Y., Guo, X. & Luo, M. (2010) Repellent effect of non-host vegetables and their extracts on *Pieris rapae* L. *Chinese Journal of Eco-Agriculture*, 18(6), 1311–1316. Available from: https://doi.org/10.3724/SP.J.1011.2010.01311

Zhang, X. & Ou, X. (2010) Fauna of some species of phytophagous ladybirds Epilachninae (Coleoptera: Coccinellidae) in Yunnan Province. *Entomotaxonomia*, 32, 53–60.

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