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8**Floral-feeding increases diet breadth in a polyphagous mirid**

9

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24Key Message

- 25● The polyphagous mirid bug, *Apolygus lucorum*, is an important pest of cotton and fruit crops.
- 26● Field density of the nymphs was higher at the flowering stage than at the vegetative stage.
- 27● Nymphs failed to develop on the vegetative tissue of some plant species, but the flowers
- 28 sustained their successful development.
- 29● The nymph survival also increased when fed on vegetative tissues with sugar.
- 30● Flowers with high sugar content allow *A. lucorum* to adapt its diet to a wider variety of plant
- 31 species.

32

33

34Abstract

35Herbivorous insect species vary significantly in the number of host plant taxa they attack. Previous
 36studies suggested host range expansion to be more likely to occur in herbivores whose immatures
 37feed on flowers due to flowers containing lower levels of plant defense compounds than vegetative
 38tissues. We tested whether the polyphagous mirid bug *Apolygus lucorum*, an important pest of
 39cotton and fruit crops, could increase its diet breadth by feeding on flowers. In field plots, the
 40density of *A. lucorum* nymphs was higher at the flowering stage than at the vegetative stage in the
 41eight plant species included in this project during 2009-2016. In two laboratory studies, adults
 42preferred to lay eggs on the plants at flowering stage over those at vegetative stage and immatures
 43failed to develop on the vegetative tissue of five of the eight species. Flowers of the same plant
 44species, however, sustained successful development of the mirid nymphs. Therefore, we compared
 45the level of secondary compounds and main nutrients in flowers and vegetative tissue of the eight
 46plant species. Six out of the eight plants tested contained lower levels of secondary metabolites in
 47flowers than in vegetative tissue, and all them contained more sugars in flowers than in vegetative
 48tissue. In a manipulative assay, *A. lucorum* nymph survival increased when fed on vegetative tissues
 49with sucrose. Hence, the higher sugar content of flowers, not just the lower content of plant defense
 50compounds, allows *A. lucorum* to adapt its diet to a wider variety of plant species.

51**Keywords** Host plant selection, Nutritional ecology, Preference-performance relationship,
 52*Apolygus lucorum*, Carbohydrates, Secondary compounds

53Introduction

54Variation in dietary specialization among species drives numerous ecological processes (Forister et
 55al. 2015). In herbivorous insects, differences in diet breadth can mediate the coexistence of
 56competitors (Büchi and Vuilleumier 2014) and the persistence of species in the face of
 57environmental disturbance (Devictor et al. 2008). By feeding at the base of the food chain,
 58phytophagous insects have access to diverse resources. However, the number of host plant taxa used
 59varies significantly and most herbivorous insects have a relatively narrow diet breadth (Jaenike
 601990). This pattern has led to the development of several hypotheses about the determination of diet
 61breadth (Thompson 1988; Jaenike 1990; Mayhew 1997; Hardy and Otto 2014; Forister et al. 2015;
 62Hardy et al. 2016). It was initially assumed that herbivores selected oviposition sites primarily on
 63the basis of plant suitability for larval development (Levins and MacArthur 1969; Mayhew 1997).
 64Although this assumption frequently fails empirical tests (Thompson 1988; Jaenike 1990;
 65Thompson and Pellmyr 1991), a meta-analysis supports the preference-performance relationship
 66(Gripenberg et al. 2010).

67 Since neonate insects are the stage most sensitive to plant quality, it was assumed that mothers
 68would select those plants that minimized neonatal mortality (i.e., plants that would increase their
 69immature stages' performance) (Zalucki et al. 2002). Upon emergence, neonates have to cope with
 70many potentially unfavorable internal or surface plant characteristics. However, plant quality for
 71herbivore insects changes with plant stage and tissue (Scriber and Slansky 1981; Awmack and
 72Leather 2002). For example, the levels of defensive secondary compounds as well as the levels of
 73nitrogen and carbohydrates vary with plant stage and tissues (Scriber and Slansky 1981; Awmack
 74and Leather 2002; Zalucki et al. 2002). Therefore, the performance of immature herbivore insects
 75can vary with plant stage and tissue.

76 Chew and Robbins (1984) suggested that insect herbivores can expand their diet breadth by
 77 feeding on flowers because flowers often contain lower levels of secondary metabolites than other
 78 organs. This mechanism would cause an increase in polyphagy if; i) adults are frequently exposed
 79 to flowers of non-hosts; ii) adult bugs occasionally oviposit on such flowers when visiting them for
 80 nectar; and iii) resulting immature stages can complete their development on these non-host
 81 flowers, presumably because defensive secondary compounds occur in flowers at relatively low
 82 levels compared to levels in leaves of such non-host plants. However, apart from potentially being
 83 less defended, flowers by virtue of their nectar and pollen are nutritionally richer than other plant
 84 tissues, especially in sugars (Wäckers et al. 2007). In addition, levels of carbohydrates and amino
 85 acids in flowers may also influence the development of immature stages and thereafter affect host
 86 plant selection by adults. Chew and Robbins's hypothesis (1984), as well as most of the empirical
 87 assays on dietary specialization and preference-performance relationships is based on lepidopterans
 88 whose adults tend to feed on nectar but not on plant tissues. When it comes to the number of host
 89 plant taxa fed upon, mirids (Hemiptera: Miridae) are another insect group in which there is a great
 90 variation on specialization (Wheeler 2001; Cassis and Schuh 2012). Moreover, in contrast to
 91 lepidopterans, mirid adults feed on plant tissues as well as nectar and pollen (Wäckers et al. 2007).

92 The mirid bug *Apolygus lucorum* (Meyer-Dür) (Hemiptera: Miridae) is an important herbivore
 93 pest in China, feeding on more than 200 plant species (Pan et al. 2015a), within this group are
 94 cotton (*Gossypium hirsutum* L.), cereals, vegetables, tea and fruit crops (Lu et al. 2008a; Lu et al.
 95 2010). During a six year study in which *A. lucorum* adult abundance was recorded on 174 plant
 96 species, adults showed a strong preference for flowering host plants and switched food plants
 97 according to the succession of flowering of plant species in the local agro-ecosystem (Pan et al.
 98 2013). Moreover, *A. lucorum* usually feeds upon buds and flowers which are often seriously

99damaged in the field (Lu and Wu 2008; Pan et al. 2013).

100 We hypothesize that *A. lucorum* has this wide diet breadth because its immature stages can feed
 101 on flowers, which are nutritionally richer than vegetative tissues. To examine this hypothesis, we
 102 first surveyed and compared the population density of *A. lucorum* nymphs on eight plant species at
 103 vegetative stage and flowering stage in field plots during 2009-2016. We then tested whether *A.*
 104 *lucorum* adults select the plant stage (floral vs. vegetative) for oviposition primarily on the basis of
 105 their suitability for juvenile performance. In parallel, we analyzed the contents of nutrients
 106 (individual sugars and amino acids) and secondary compounds (tannins and flavonoids) in flowers
 107 and young leaf tissue. The aim was to test whether the variations of these two nutrients and
 108 secondary compounds explain the observed differences in oviposition levels and nymphal
 109 performance between both plant tissues. With all these results, a final manipulative assay was
 110 carried out to determine which nutrient/secondary compound influences or promotes the wide diet
 111 breath of *A. lucorum*.

112

113 **Materials and methods**

114 **Insects and plants**

115 A laboratory colony of *A. lucorum* was started with approximately 2,000 adults and nymphs
 116 collected from cotton fields at Langfang Experimental Station, Chinese Academy of Agricultural
 117 Sciences (CAAS; 39.53°N, 116.70°E) (Langfang, Hebei Province) in July and August, 2013-2016.
 118 These mirid bugs were reared on green bean pods (*Phaseolus vulgaris* L.) and provided a cotton
 119 ball soaked with a 10% honey solution, as described by Lu et al. (2008b). Second and third
 120 generation individuals were used for the trials.

121 Based on our previous field studies (Pan et al. 2013), eight species of host plants; *Agastache*

122 *rugosus* (Fisch. et Meyer) O. Kuntze., *Artemisia argyi* Lévl. et Vant., *Artemisia lavandulaefolia* DC.,
 123 *Cannabis sativa* L., *Humulus scandens* (Lour.) Merr., *Mentha haplocalyx* Briq., *Ocimum basilicum*
 124 L. and *Schizonepeta tenuifolia* (Benth.) Briq., were chosen because they typically sustain abundant
 125 *A. lucorum* adult population during flowering stage. Wild plants (*H. scandens* and *Artemisia* spp.)
 126 were transplanted as seedlings from neighboring agricultural fields, while seeds for the other plants
 127 were obtained from the Institute of Vegetables and Flowers, CAAS (Pan et al. 2013). Planting took
 128 place on two separate occasions (early May and late June) by direct seeding or transplanting to the
 129 field at the Langfang Experiment Station of CAAS. This staggered planting allowed us to compare
 130 flowering and vegetative stages of each plant side by side. Plants were managed using identical
 131 agronomic practices, without insecticides (Lu et al. 2010). All plants were caged (80 mesh) to
 132 prevent damage by herbivorous insects and mites before the trial. Vegetative (ca. 2 weeks before
 133 the first emergence of flower buds) and flowering periods (peak bloom) of each plant species were
 134 used for this study.

135 Field trials

136 During 2009-2016, population density of *A. lucorum* nymphs on the eight plant species above
 137 mentioned were examined in field plots at the Langfang Experiment Station of CAAS. Each plant
 138 species was established in three individual 4 m × 4 m plots every year in the beginning of May. All
 139 plots were arranged randomly and embedded within hundreds of plots. All plots were separated by a
 140 1 m space that was kept free of vegetation by hand weeding. Plants were managed using identical
 141 agronomic practices, without insecticides (Pan et al. 2013).

142 Every year we surveyed the abundance of *A. lucorum* nymphs within each field plot every 5-7
 143 days from early July to mid-September. The protocols used were those similar to Pan et al. (2013).

144 Sampling consisted of visual plant inspections to detect the presence of *A. lucorum* nymphs,

complemented by knock-down techniques, which consisted of holding the plant over a rectangular $40 \times 26 \times 11$ cm white-colored pan and striking the plant four times, afterwards the number of dislodged *A. lucorum* nymphs of different instars was recorded, and then the nymphs were returned to the sampling site. During each sample date, we determined the number of *A. lucorum* nymphs by adding the counts obtained from visual plant inspections and knock-down techniques. The identification of the nymphal instars was based on their morphological features (Lu and Wu 2008). Four 1×1 m subplots were sampled within each plot. The growth stage and the presence of flowers for each plant species included in the trial were also recorded during each sampling date (Pan et al. 2013).

Oviposition preference on the distinct plants at vegetative and flowering stages

Oviposition preference of female *A. lucorum* was determined by paired-choice experiments in the laboratory, the methods used were similar to Dong et al. (2013). When a given plant was in full bloom branches with flowers (100 g) were cut with scissors and immediately put into a corner of a one 1 m^3 cage (80 mesh). In the opposite corner of the same cage, we then introduced branches (also 100 g) cut from the same plant species but from individuals still in the pre-flowering vegetative period. Cut ends of all the branches were wrapped with moist cotton towels and enclosed inside a plastic bag before they were placed in the cage. Six mated females (8-10 days old) were released in the centre of each cage. After 24 h, plant materials were collected and dyed with a 1% eosin solution (Beijing Chemical Works) for two min to dye eggs (Dong et al. 2012), and thereafter the number of eggs laid on each plant was determined through observation with a microscopic (Olympus). For this experiment, there were six replicates for each plant species.

Nymphal performance on the distinct plant tissues

Nymphal performance was assessed by placing newly emerged first instar nymphs, collected from

the laboratory colony, individually into glass vials (3 cm long, 3 cm diam., covered with a nylon screen). Each vial contained either excised flowers or vegetative terminals; each treatment was provided approximately the same amount of plant biomass for each plant species (Dong et al. 2013). Experiments were conducted at 25°C in growth chambers (RXZ-500C, Ningbo Jiangnan Instrument Factory, Ningbo, China) with a 14:10 (L:D) photoperiod and 65% RH. Feed plants were changed daily. In each treatment 100-120 individual bugs, as replicates, were employed for every plant species evaluated. Nymphal development and adult emergence were recorded daily until they either died or molted into the adult stage. The adult sex ratio and weight were also determined.

Sugar and amino acid levels in the distinct plant tissues

Flowers and tender leaf tips from each plant species evaluated were dried at 80 °C for two days until a constant dry weight (DW) was attained at which time they were ground into powder. Analyses and quantification of fructose, glucose, maltose, and sucrose were performed using a high-performance liquid chromatography-refractive index (HPLC-RI) system. Briefly, 30 mg of DW was dissolved in 0.7 ml of 80% ethanol to extract the sugars. The sample was thoroughly mixed with a vortex and incubated for 2 h at 70 °C. Aliquots of 0.7 ml of HPLC-grade water and 0.7 ml chloroform were added to the sample. After shaking several times, the mixture was centrifuged at 12,000 g for 5 min. Then, 1 ml of the aqueous supernatant was transferred into 1.5-ml Eppendorf tubes and re-suspended in 0.7 ml of chloroform. After centrifugation at 12,000 g for 10 min, 0.5 ml of the supernatant was transferred to a glass tube for HPLC analysis of each sugar component with an injection volume of 10 µl. The sugar-separation method used was that described by the manufacturer with the exception of the Agilent technologies HPLC column (ZORBAX Carbohydrate column; 4.6 × 150 mm, 5 µm) with a differential refraction detector. The mobile phase consisted of 75% acetonitrile with a flow rate of 0.8 ml/min. The temperature of the column

191 was maintained at 35 °C. Four types of sugars that naturally occur in the flowers, i.e. D-(-)-fructose
 192 (Sigma), D-glucose (Amresco), D-(+)-maltose (Sigma), and sucrose (Amresco) (all sugars were $\geq$
 193 99% pure), were identified based on the retention time of standards, and sample concentrations
 194 were calculated from the external standard curve. Three replicates of both flowers and tender leaf
 195 tips were evaluated for each plant species.

196 As for amino acid content, plant flowers and tender leaf tips were selected and powder was
 197 produced from them as described above. For both plant organs, twenty mg of dried powder was
 198 dissolved in 1 ml of 6 M HCl. The sample was thoroughly mixed with a vortex and incubated for 21
 199 h at 105 °C. Following acidolysis, the mixture was centrifuged at 12,000 g for 10 min, after which
 200 1 ml of the aqueous supernatant was dried in a vacuum concentrator (Eppendorf, Hamburg,
 201 Germany). The dried samples were re-dissolved in 0.5 ml of 0.1 N HCl. After centrifugation at
 202 12,000 g for 10 min once again, the supernatant was transferred to a glass tube for HPLC analysis
 203 of each amino acid component with an injection volume of 1 μ l. The Agilent technologies HPLC
 204 column (ZORBAX Eclipse column; 4.6 $\times$ 150 mm, 3.5 μ m) with a UV detector was used. The
 205 detection wave length was fixed to 383 nm. The separation method followed was that described by
 206 the instructions for the column. The amino acids were identified based on the retention time of the
 207 standards (LAA21, Sigma, St. Louis, MO, USA), and sample concentrations were calculated from
 208 the external standard curve (Davidson 2003). Three replicates of both flowers and tender leaf tips
 209 were made for each species.

210 Secondary compounds levels in the distinct plant tissues

211 Defense compounds contained in cotton plants and their resistant effects on *A. lucorum* have been
 212 widely reported (Lin et al. 2011; Luo et al. 2012), whereas limited information on defense
 213 compounds from wild plants (e.g., *H. scandens* and *Artemisia* spp.) is available. Hence, we further

214analyzed and compared defense compounds (tannins and flavonoids) in the flowers and vegetative
215tissues of the eight plant species included in this study.

216 The content of tannins contained in the flowers and tender leaf tips of the eight plant species
217were determined following the ISO 9648 methodology. A 200 mg dried sample of each of the two
218plant organs for each species was dissolved in 10 ml of 75% dimethylformamide (DMF) solution,
219thoroughly mixed with a vortex and then incubated at 25-30°C for 1 h. After incubation the samples
220were centrifuged, the supernatant removed, and then stored in the dark. To accurately absorb the
221tannin extract in test tube 1, distilled water and ammonia solution were added, the solution was
222thoroughly mixed then incubated for 10 min at 25-30°C. The absorbance value A1 of the sample
223solution was measured at a wavelength of 525 nm using a spectrophotometer. To accurately extract
224the tannins in test tube 2, distilled water, ferric ammonium citrate solution oscillation, plus ammonia
225solution were added. The solution was thoroughly mixed then incubated for 10 min at 25-30°C. The
226absorbance value A2 of the sample solution was measured at 525 nm with distilled water as a blank.
227The tannin concentration in the sample is $A = A_2 - A_1$. The quantification of tannins was acquired
228with the standard curve that was obtained by using diverse tannic acid concentrations. Three
229replicates of both flowers and tender leaf tips were evaluated for each plant species.

230 The total flavonoid content in the flowers and tender leaf tips of the eight plant species was
231determined by the aluminium chloride colorimetric method (Chang et al. 2002). In brief, 50 µl of
232crude extract (1 mg/ml ethanol) were made with 1 ml of methanol, mixed with 4 ml of distilled
233water and then 0.3 ml of 5% NaNO₂ solution; 0.3 ml of 10% AlCl₃ solution was added after 5 min
234of incubation; then the mixture was allowed to stand for 6 min. Next, 2 ml of 1 mol/l NaOH
235solution was added, and the final volume of the mixture was brought to 10 ml with double-distilled
236water. The mixture was allowed to stand for 15 min; thereafter, absorbance was measured at 510

237nm. The total flavonoid content was calculated from a calibration curve, and the result was
 238expressed as mg rutin equivalent per g dry weight (Baba and Malik 2015). Three replicates of both
 239flowers and tender leaf tips were evaluated for each of the eight plant species.

240**Nymphal performance on individual saccharides**

241Both sugars and amino acids are important nutrients for immature phytophagous insects (Scriber
 242and Slansky 1981). Based on the results obtained in the previous sections (see Results), we inferred
 243that increasing sugar content, rather than decreased amino acid content, might be the key factor
 244determining the greater level of *A. lucorum* nymph fitness on flowers than on tender leaf tips. We
 245therefore determined the effect of the distinct sugars on *A. lucorum* nymphal performance.

246 First, a 1 M concentration solution for each sugar (fructose, glucose, maltose, and sucrose) was
 247diluted with distilled water; distilled water was also used as the control. Green bean pods (3 cm
 248long) were soaked in one of the sugar solutions for three minutes and allowed to dry for one hour in
 249the laboratory. Finally, the pods were wrapped in paraffin film to avoid the innate risk of the sugar
 250viscosity on *A. lucorum* nymphs. Feng et al. (2012) reported that *A. lucorum* can normally feed on
 251artificial diets wrapped in paraffin film. Our preliminary trial also found this to be true; the mirid
 252bug can indeed feed and develop on green beans wrapped in paraffin film. Thus, nymphal
 253performance on wrapped green bean pods soaked in the various sugar solutions was assessed using
 254the above mentioned method.

255**Nymphal performance on tender leaf tips with sucrose**

256Based on the results obtained in the previous sections (see Results), we hypothesized that sucrose in
 257flowers is the key factor determining the improved fitness of *A. lucorum* nymphs compared to that
 258in vegetative organs. To test this, nymphal performance on the tender leaf tips of the eight plant
 259species with and without sucrose was assessed using the same method mentioned above. To obtain

tender leaf tips with sucrose, the tips were soaked in a 1 M sucrose solution for three minutes at which time they were allowed to dry for one hour in the laboratory before using them.

Statistical analysis

We performed a two-way ANOVA to analyze the variation of abundance of *A. lucorum* nymphs across different sampling years, growth stages, and the interaction among them. Sampling plot was the random factor. Nymphal abundance was arcsine transformed before subjecting the data to analyses. Paired t-tests were employed to compare the number of eggs laid on flowering versus vegetative plants for each plant species in the oviposition cage trials, data were square-root transformed before analysis. Nymphal survival rates between different plant foods within species were analyzed with a χ^2 goodness-of-fit test. Non-paired t-tests were employed to compare nymphal developmental duration and adult *A. lucorum* weight between plant flowers and tender leaf tips for each species, and between tender leaf tips with and without sucrose. Paired t-tests were used to compare the contents of nutrient substances (sugars and amino acids) and secondary compounds (tannins and flavonoids) in plant flowers versus tender leaf tips. Principal component analysis (PCA) was used to examine the sugar composition of the flowers of all eight host plants, and PC1 and PC2 scores were compared among the eight host plants. The effects of the four sugars on nymphal survival rates, developmental duration, and adult *A. lucorum* female and male weights were all analyzed using a one-way ANOVA followed by Tukey's HSD for multiple comparisons. All statistical analyses were performed using SAS programs (SAS 2005).

279

Results

Population abundance of *A. lucorum* nymphs on the eight plant species in field plots

In field plots, the numbers of *A. lucorum* nymphs on each of the eight host plants (*A. rugosus*, *A.*

283 *argyi*, *A. lavandulaefolia*, *C. sativa*, *H. scandens*, *M. haplocalyx*, *O. basilicum* and *S. tenuifolia*)

284 were significantly lower in the vegetative stage than in the flowering stage during 2009-2016 (Table
285 1). Moreover, the interaction between year and plant growth stage were all significant ($P < 0.05$ for
286 each plant species).

287 **Oviposition preference of *A. lucorum* adults on the distinct plants at vegetative and flowering** 288 **stages**

289 In the caged choice experiments, female *A. lucorum* adults preferred to lay eggs significantly more
290 on plants at the flowering stage compared with those in the vegetative stage for each of eight plant
291 species evaluated (all $P < 0.05$ for each host plant species tested) (Fig. 1).

292 **Performance of *A. lucorum* nymphs on the distinct plant tissues**

293 For each of the above eight host plants, the immature survival rate, male and female developmental
294 period of nymphs, and male and female adult weights were all significantly higher when reared on
295 flowers compared with individuals reared on tender leaf tips (all $P < 0.05$). In contrast, the sex ratio
296 between distinct plant foods within each plant species was not significantly different (all $P > 0.05$)
297 (Table 2; Table S1).

298 **Sugar and amino acid content of the distinct plant tissues**

299 For all eight host plants, total sugar content was significantly higher in flowers than in tender leaf
300 tips (all $P < 0.05$) (Table 3; Table S2). More specifically, except for *A. lavandulaefolia* ($P > 0.05$),
301 fructose and glucose were higher in the flowers than in the tender leaf tips of the other seven plant
302 species ($P < 0.05$). As for maltose content, except for *H. scandens*, *M. haplocalyx* and *S. tenuifolia*
303 ($P > 0.05$), a significant difference was found between the flowers and tender leaf tips of the other
304 five host plants ($P < 0.05$). Finally, sucrose content was higher in flowers than in tender leaf tips of
305 all eight species ($P < 0.05$) (Table 3; Table S2). Meanwhile, the total amino acid content was lower

306in flowers compared to tender leaf tips ($P < 0.05$) (Table 3; Table S2), and a similar trend was
 307found in many individual amino acid levels in the diverse host plants (Table S3).

308 PCA identified two principal components (PC1 and PC2) that accounted for 40.0% and 31.6%
 309of the overall variance in sugar composition, respectively. Positive values of PC1 indicated flowers
 310contained a high content of fructose, glucose, and maltose. Positive values of PC2 indicated flowers
 311contained a high content of sucrose, and negative values of PC2 were explained primarily by
 312maltose. Scores for PC1 and PC2 were significantly different among the eight host plants (PC1:
 313 $F_{7,16} = 126.40$, $P < 0.0001$; PC2: $F_{7,16} = 110.59$, $P < 0.0001$), indicating significant differences in
 314flower sugar composition among the eight species (Fig. S1).

315The content of secondary compounds in the distinct plant tissues

316Tannin content in flowers of three plant species (*A. argyi*, *A. lavandulaefolia* and *H. scandens*) was
 317significantly lower than in tender leaf tips (all $P < 0.05$), whereas in the flowers of *A. rugosus*, *M.*
 318*haplocalyx*, *O. basilicum* and *S. tenuifolia* it was higher (all $P < 0.05$). There were non-significant
 319differences between the flowers and tender leaf tips of *C. sativa* ($P > 0.05$). The content of
 320flavonoids in the flowers of four plant species (*A. argyi*, *M. haplocalyx*, *O. basilicum* and *S.*
 321*tenuifolia*) were significantly lower than in tender leaf tips (all $P < 0.05$), whereas there were not
 322significant differences in the other four tested plant species (*A. rugosus*, *A. lavandulaefolia*, *C.*
 323*sativa* and *H. scandens*) (all $P > 0.05$) (Table 3; Table S2).

324Nymphal performance of *A. lucorum* on individual saccharides

325When provided with green bean pods soaked in each sugar or a distilled water control, the survival
 326rate of *A. lucorum* was different among treatments ($F_{4,15} = 16.73$, $P < 0.0001$); survival was the
 327highest in the sucrose treatment. However, no differences were detected among fructose, maltose,
 328and the water control ($P > 0.05$). Sucrose significantly shortened the *A. lucorum* female

developmental duration compared to the other treatments ($F_{4,137} = 8.98$, $P < 0.0001$), except between maltose and the water control where there was no difference ($P > 0.05$). Meanwhile, the sucrose treatment also presented significantly shortened developmental time for male bugs compared with the other treatments ($F_{4,141} = 5.48$, $P = 0.0004$). There were no significant differences in male developmental times among the other three sugars and the control ($P > 0.05$). The sucrose, fructose, and glucose treatments all showed a significant increase in the *A. lucorum* female weight compared with the maltose treatment or the control ($F_{4,137} = 12.83$, $P < 0.0001$). Meanwhile, only sucrose and glucose treatments showed an increased *A. lucorum* male weight ($F_{4,141} = 10.70$, $P < 0.0001$), with no significant differences among fructose, maltose, and the water control treatments ($P > 0.05$). In addition, sex ratio was not significantly different among the four sugar treatments and the water control ($P > 0.05$) (Table S4).

Nymphal performance of *A. lucorum* on tender leaf tips with and without sucrose

Immature survival and adult *A. lucorum* weight were significantly higher when reared on tender leaf tips with sucrose rather than without, in all eight plant species (all $P < 0.05$) (Table 4; Table S5). Immature developmental time of *A. lucorum* females was significantly shorter when they fed on tender leaf tips of *A. rugosus*, *C. sativa*, *M. haplocalyx*, *O. basilicum* and *S. tenuifolia* with sucrose than without (all $P < 0.05$). There were no significant differences for the other three plant species (all $P > 0.05$). The addition of sucrose also reduced the developmental time of males in four host plants (*A. rugosus*, *C. sativa*, *M. haplocalyx* and *O. basilicum*) (all $P < 0.05$), whereas there were no differences for the other plant species (all $P > 0.05$). Finally, the sex ratio of *A. lucorum* did not differ between treatments within any of the plant species (all $P > 0.05$) (Table 4; Table S5).

350

Discussion

352 *Apolygus lucorum* may have expanded its diet breadth by feeding on flowering plants of species
 353 that would not otherwise sustain its growth and development. For example, immature stages of this
 354 phytophagous mirid could not develop on vegetative tissues of *A. rugosus* and *M. haplocalyx*, and
 355 nymphal development was very marginal on the non-flowering foliage of *C. sativa*, *O. basilicum*
 356 and *S. tenuifolia*. Adults circumvented this constraint by laying their eggs in flowering plants of the
 357 same plant species, where their immatures successfully developed. The fact that *A. lucorum* adults
 358 selected flowering plants to oviposit supports the preference-performance hypothesis (Mayhew
 359 1997). These laboratory observations are highly consistent with our eight-year-field study and
 360 previous studies. Almost no *A. lucorum* nymphs were found on the plant species during the seedling
 361 (pre-flowering) period, whereas nymphal abundance greatly increased after plants reached the
 362 flowering stage. The same pattern was also found when *A. lucorum* had access to flowering and
 363 non-flowering plants of cotton, balsam (*Impatiens balsamina*), or castor bean (*Ricinus communis*)
 364 (Dong et al. 2013). Although the highest abundance of *A. lucorum* nymphs during the flowering
 365 period could also be explained by the phenological synchronization of *A. lucorum* and the plants,
 366 several studies relating to other mirid bugs, such as three *Adelphocoris* species (Gao et al. 2014) and
 367 *Lygus lineolaris* (Palisot de Beauvois) (Abel et al. 2010), also support a positive preference-
 368 performance relationship in the Miridae. Altogether, these studies suggest that this positive
 369 relationship is likely to be universal for phytophagous mirids.

370 Our results partially agree with the hypothesis by Chew and Robbins (1984) for lepidopterans.
 371 They suggest that host range expansion is likely in herbivores whose immature stages feed on
 372 flowers, given that flowers often contain lower levels of secondary metabolites; however, Stevenson
 373 et al. (2017) presents exceptions that nectar of some plant species contain higher levels of secondary
 374 metabolites, which maybe toxic or repellent to herbivores. In our study, six out of the eight plants

375 included in this study contained lower levels of either tannins or flavonoids in the flowers than in
 376 the leaf tips. Therefore, the lower concentration of secondary metabolites in flowers can, at least
 377 partially, explain the selection of flowering plants by *A. lucorum* adults and the higher survival rate
 378 of immature individuals developed on plants in this stage. As exceptions, the flowers of *A. rugosus*
 379 and *O. basilicum* allowed the development of *A. lucorum*, even though they contained the same or
 380 even higher concentrations of metabolites than the leaf tips. The higher concentration of sugars in
 381 flowers than in tender leaves can also explain the higher performance of immatures in flowering
 382 plants.

383 In the eight plants analyzed in this study, the levels of sugars and amino acids differed
 384 quantitatively and qualitatively between flowers and vegetative tissues. It has been generally
 385 assumed that nitrogen content is an important determinant of neonate performance in insects
 386 (Mattson 1980; Han al. 2014; 2016; Horgan et al. 2018; Blazhevski et al. 2018). However, we found
 387 that sugar content, not amino acid content, correlated positively with immature performance as
 388 sugar content was higher in flowers. When we analyzed the main sugars in the flowers of all eight
 389 plant species, sucrose content was lower than that of glucose, fructose, and maltose, but sucrose by
 390 itself explained 31.6% of the overall variance in the sugar composition of flowers. Moreover, in the
 391 subsequent bioassay, *A. lucorum* had the highest performance when fed on this sugar. The
 392 zoophytophagous mirid *Nesidiocoris tenuis* (Reuter) (Hemiptera: Miridae) also had improved
 393 nymphal developmental and survival when 0.5 M sucrose was added to its diet (Urbaneja-Bernat et
 394 al. 2013). Moreover, *A. lucorum* nymph survival was higher in all the plant species when they had
 395 access to tender leaf tips with sucrose. Overall, our physiological analysis and subsequent
 396 manipulative assay demonstrated that phytophagous mirids increase their performance by feeding
 397 on flowers instead of vegetative tissues, and this increase in performance is also due to the higher

sugar content, mainly sucrose. Therefore, not only the lower content of plant defense compounds are found in some flowers, as suggested by Chew and Robbins (1984), but also their higher concentration in sucrose compared to vegetative tissues, might allow expansion of diet breadth in mirids.

In our study, we did not determine whether the immature stages fed on flower tissues or nectar and pollen. In the field, flower tissues suffer the most serious damage, suggesting that *A. lucorum* nymphs feed on them (Lu and Wu 2008; Pan et al. 2013). However, nectar and pollen feeding cannot be disregarded because some mirid species have been observed feeding on these resources. For example, the mirid *Lygocoris pabulinus* L. can be found visiting flowers, apparently feeding on nectar (Wheeler 1996), and *L. lineolaris* was also found in significantly higher numbers in nectar-producing cotton than in nectar-less cotton (Schuster et al. 1976; Scott et al. 1988). In any case, flower tissue, nectar, and pollen are all less defended resources than vegetative stems and foliage (Wäckers et al. 2007). Flowering and vegetative tissues differ not only in the levels of plant defense compounds involved in resistance to insect herbivory but also in the principal nutrients needed by insects (Scriber and Slansky 1981; Awmack and Leather 2002).

Generalists are considered less efficient than specialists at choosing host plants accurately and generally need more time to select because they must integrate information from different stimuli (Bernays 2001). In the case of *A. lucorum*, however, the mirid might have simplified the problem by enhancing its sensitivity to general flower compounds. Our caged experiments suggest that *A. lucorum* females have a significant oviposition preference for plants with flowers, independent of plant species. Moreover, an olfactory receptor, which is sensitive to several flowering compounds, has been recently identified and characterized in *A. lucorum* (Yan et al. 2015). These results are consistent with previous field findings that host plants that are in flower typically bear larger

421populations of *A. lucorum* adults than do plants at the non-flowering stage (Pan et al. 2013). Y-tube
 422olfactometer trials show that adults of this species prefer flower volatiles to volatiles from tender
 423leaf tips of the same plant species, and indeed prefer four specific volatile fragrances (Pan et al.
 4242015b). Therefore, the use of general flower compounds may have contributed to the expansion of
 425diet breadth in mirids by decreasing the amount of information that adults have to process to select
 426or reject species as hosts.

427

428**Author contribution statement**

429HP, YL, AT and ND conceived and designed the experiments. HP, CX and BL performed the
 430experiments. HP, YL, BL, AT and ND analyzed the data. HP, YL, AT and ND wrote the paper. All
 431authors read and approved the manuscript.

432

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438

439**Compliance with ethical standards**

440**Conflict of interests** The authors declare that they have no conflict of interest.

441**Ethical approval** All applicable international, national and institutional guidelines for the care and
 442use of animals were considered in the present study.

443**Informed consent** The six authors of this manuscript accepted that the paper is submitted for

444 publication in the Journal of Pest Science, and reported that this paper has not been published or
 445 accepted for publication in another journal, and it is not under consideration at another journal.

446

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- 549

550**Table 1. Average density of *Apolygus lucorum* nymphs on eight plant species at flowering and vegetative stages in field plots during 2009-2016**

Year	Growth stage	<i>Agastache rugosus</i>	<i>Artemisia argyi</i>	<i>Artemisia lavandulaefolia</i>	<i>Cannabis sativa</i>	<i>Humulus scandens</i>	<i>Mentha haplocalyx</i>	<i>Ocimum basilicum</i>	<i>Schizonepeta tenuifolia</i>
2009	Vegetative stage	ND	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.07 ± 0.07	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
	Flowering stage	ND	2.33 ± 0.70	1.58 ± 0.46	0.33 ± 0.00	7.00 ± 1.00	3.83 ± 0.63	3.78 ± 0.48	0.67 ± 0.19
2010	Vegetative stage	0.07 ± 0.07	0.06 ± 0.06	0.67 ± 0.35	0.04 ± 0.04	0.25 ± 0.14	0.00 ± 0.00	0.11 ± 0.11	0.20 ± 0.00
	Flowering stage	1.96 ± 0.29	6.53 ± 1.13	6.71 ± 0.97	2.83 ± 0.85	4.33 ± 0.78	3.00 ± 0.55	4.87 ± 0.35	2.75 ± 0.47
2011	Vegetative stage	0.13 ± 0.07	0.25 ± 0.19	0.13 ± 0.00	0.07 ± 0.04	0.07 ± 0.07	0.17 ± 0.17	0.67 ± 0.00	0.33 ± 0.10
	Flowering stage	0.63 ± 0.00	2.00 ± 0.23	3.07 ± 0.18	0.33 ± 0.17	3.42 ± 0.75	1.11 ± 0.22	2.67 ± 0.20	2.94 ± 0.24
2012	Vegetative stage	0.00 ± 0.00	0.48 ± 0.05	0.79 ± 0.33	0.00 ± 0.00	0.33 ± 0.13	ND	0.00 ± 0.00	ND
	Flowering stage	1.20 ± 0.23	17.72 ± 2.90	16.20 ± 3.30	7.92 ± 1.38	9.38 ± 1.55	ND	4.18 ± 0.50	ND
2013	Vegetative stage	0.15 ± 0.10	0.03 ± 0.03	0.21 ± 0.03	0.26 ± 0.13	0.03 ± 0.03	0.33 ± 0.00	0.00 ± 0.00	0.03 ± 0.03
	Flowering stage	0.67 ± 0.17	4.11 ± 1.13	2.83 ± 0.36	0.84 ± 0.17	1.33 ± 0.08	0.22 ± 0.06	1.74 ± 0.47	2.42 ± 0.68
2014	Vegetative stage	0.03 ± 0.03	0.12 ± 0.08	0.27 ± 0.16	0.21 ± 0.15	0.00 ± 0.00	0.37 ± 0.13	0.11 ± 0.11	0.67 ± 0.17
	Flowering stage	0.83 ± 0.22	19.83 ± 3.71	10.58 ± 1.42	1.29 ± 0.14	8.75 ± 1.51	0.45 ± 0.15	2.92 ± 0.27	3.30 ± 0.49
2015	Vegetative stage	ND	0.05 ± 0.05	0.14 ± 0.00	0.11 ± 0.06	0.38 ± 0.13	0.28 ± 0.05	0.00 ± 0.00	0.00 ± 0.00
	Flowering stage	ND	2.11 ± 0.22	3.00 ± 0.33	0.83 ± 0.44	2.11 ± 0.11	1.00 ± 0.29	2.00 ± 0.26	2.95 ± 0.13
2016	Vegetative stage	ND	0.19 ± 0.13	0.14 ± 0.00	0.33 ± 0.07	0.13 ± 0.13	0.13 ± 0.13	0.11 ± 0.11	0.08 ± 0.08
	Flowering stage	ND	1.33 ± 0.51	1.89 ± 0.80	0.87 ± 0.24	2.73 ± 0.35	0.47 ± 0.07	1.95 ± 0.17	3.22 ± 0.58
Statistical values of two- way ANOVA	Year	$F = 4.13, df = 4, 20, P = 0.0134$	$F = 25.3, df = 7, 32, P < 0.0001$	$F = 18.12, df = 7, 32, P < 0.0001$	$F = 12.98, df = 7, 32, P < 0.0001$	$F = 13.99, df = 7, 32, P < 0.0001$	$F = 9.53, df = 6, 28, P < 0.0001$	$F = 9.06, df = 7, 32, P < 0.0001$	$F = 5.40, df = 6, 28, P = 0.0008$
	Growth stage	$F = 158.41, df = 1, 20, P < 0.0001$	$F = 615.07, df = 1, 32, P < 0.0001$	$F = 405.55, df = 1, 32, P < 0.0001$	$F = 144.31, df = 1, 32, P < 0.0001$	$F = 820.26, df = 1, 32, P < 0.0001$	$F = 136.71, df = 1, 28, P < 0.0001$	$F = 1027.7, df = 1, 32, P < 0.0001$	$F = 202.22, df = 1, 28, P < 0.0001$
	Year*Growth stage	$F = 6.39, df = 4, 20, P = 0.0018$	$F = 19.74, df = 7, 32, P < 0.0001$	$F = 7.34, df = 7, 32, P < 0.0001$	$F = 16.28, df = 7, 32, P < 0.0001$	$F = 14.04, df = 7, 32, P < 0.0001$	$F = 21.96, df = 6, 28, P < 0.0001$	$F = 9.5, df = 7, 32, P < 0.0001$	$F = 3.27, df = 6, 28, P = 0.0146$

551 “ND” means no data is available for this plant species in this year.

552**Table 2. Effect of plant tissues (flowers vs. tender leaf tips) on nymphal survival, development and *Apolygus lucorum* adult weight**

Host plants	Plant tissues	Survival rate (%)	Developmental duration (days)		Sex ratio (female/female+male)	Weight (mg)	
			Female	Male		Female	Male
<i>Agastache rugosus</i>	Tender leaf tips	0	0	0	0	0	0
	Flowers	80.91 ± 7.07	13.58 ± 0.17	13.05 ± 0.14	0.55 (48/88)	4.37 ± 0.11	3.98 ± 0.11
<i>Artemisia argyi</i>	Tender leaf tips	61.67 ± 3.97 b	17.16 ± 0.28 a	16.08 ± 0.23 a	0.51 (38/74)	2.61 ± 0.10 b	2.51 ± 0.10 b
	Flowers	78.33 ± 5.53 a	14.60 ± 0.30 b	13.94 ± 0.24 b	0.43 (40/94)	4.28 ± 0.13 a	3.74 ± 0.11 a
<i>Artemisia lavandulaefolia</i>	Tender leaf tips	61.67 ± 4.41 b	16.32 ± 0.21 a	16.18 ± 0.28 a	0.55 (41/74)	2.81 ± 0.10 b	2.58 ± 0.12 b
	Flowers	77.50 ± 2.10 a	14.33 ± 0.23 b	14.02 ± 0.20 b	0.49 (46/93)	4.04 ± 0.13 a	3.80 ± 0.11 a
<i>Cannabis sativa</i>	Tender leaf tips	15.90 ± 2.92 b	14.10 ± 0.35 a	13.63 ± 0.46 a	0.56 (10/18)	1.65 ± 0.23 b	1.89 ± 0.15 b
	Flowers	94.08 ± 0.83 a	11.43 ± 0.09 b	11.18 ± 0.11 b	0.55 (61/111)	4.85 ± 0.09 a	4.07 ± 0.08 a
<i>Humulus scandens</i>	Tender leaf tips	68.33 ± 5.00 b	15.43 ± 0.19 a	14.80 ± 0.17 a	0.45 (37/82)	3.00 ± 0.09 b	3.01 ± 0.08 b
	Flowers	90.83 ± 0.83 a	12.21 ± 0.19 b	11.91 ± 0.11 b	0.48 (52/109)	5.07 ± 0.12 a	4.63 ± 0.08 a
<i>Mentha haplocalyx</i>	Tender leaf tips	0	0	0	0	0	0
	Flowers	43.18 ± 2.69	12.87 ± 0.14	12.22 ± 0.17	0.46 (23/50)	3.91 ± 0.14	3.06 ± 0.11
<i>Ocimum basilicum</i>	Tender leaf tips	20.83 ± 2.50 b	15.89 ± 0.77 a	14.94 ± 0.40 a	0.36 (9/25)	2.79 ± 0.34 b	2.41 ± 0.17 b
	Flowers	89.17 ± 3.44 a	13.25 ± 0.15 b	12.76 ± 0.17 b	0.50 (53/107)	4.41 ± 0.10 a	4.12 ± 0.08 a
<i>Schizonepeta tenuifolia</i>	Tender leaf tips	21.32 ± 2.41 b	19.23 ± 0.51 a	17.83 ± 0.44 a	0.52 (13/25)	1.42 ± 0.13 b	1.38 ± 0.16 b
	Flowers	79.15 ± 2.10 a	11.30 ± 0.08 b	11.39 ± 0.08 b	0.48 (46/95)	3.37 ± 0.05 a	3.15 ± 0.07 a

553Means (± SE) followed by different letters illustrate significant differences between flowers and tender leaf tips within each plant species ($P < 0.05$).

554**Table 3. The content of sugar, total amino acid and secondary compounds in the flowers and tender leaf tips of the eight plant species**

Host plants	Plant tissues	Content (ug/mg)							
		Fructose	Glucose	Maltose	Sucrose	Total sugars	Total amino acids	Tannins	Flavonoids
<i>Agastache rugosus</i>	Tender leaf tips	18.93 ± 0.34 b	44.43 ± 0.27 b	13.80 ± 0.58 b	0.11 ± 0.01 b	77.28 ± 0.48 b	226.26 ± 0.55 a	0.26 ± 0.02 b	4.14 ± 0.23 a
	Flowers	34.99 ± 0.33 a	64.18 ± 0.13 a	17.71 ± 0.03 a	2.94 ± 0.04 a	119.82 ± 0.47 a	186.59 ± 0.75 b	2.85 ± 0.30 a	6.69 ± 1.18 a
<i>Artemisia argyi</i>	Tender leaf tips	11.52 ± 0.22 b	7.01 ± 0.19 b	5.51 ± 0.12 b	1.58 ± 0.09 b	25.62 ± 0.14 b	219.87 ± 5.01 a	12.25 ± 0.52 a	23.75 ± 0.12 a
	Flowers	19.70 ± 0.05 a	14.99 ± 0.27 a	6.41 ± 0.07 a	5.15 ± 0.10 a	46.25 ± 0.44 a	197.29 ± 5.64 b	3.41 ± 0.06 b	16.50 ± 0.79 b
<i>Artemisia lavandulaefolia</i>	Tender leaf tips	17.42 ± 0.07 a	13.36 ± 0.16 a	2.56 ± 0.06 b	2.06 ± 0.07 b	35.42 ± 0.15 b	231.94 ± 6.50 a	5.58 ± 0.33 a	14.50 ± 0.99 a
	Flowers	17.36 ± 0.23 a	13.61 ± 0.14 a	5.33 ± 0.18 a	4.97 ± 0.35 a	41.27 ± 0.27 a	190.23 ± 0.77 b	2.91 ± 0.10 b	13.60 ± 0.28 a
<i>Cannabis sativa</i>	Tender leaf tips	22.68 ± 0.18 b	17.66 ± 0.22 b	15.98 ± 0.26 a	0.53 ± 0.09 b	56.85 ± 0.45 b	296.05 ± 3.55 a	2.47 ± 0.09 a	12.32 ± 0.60 a
	Flowers	38.75 ± 0.28 a	37.21 ± 0.09 a	8.41 ± 0.17 b	9.91 ± 0.28 a	94.29 ± 0.48 a	225.96 ± 8.58 b	2.19 ± 0.15 a	14.17 ± 0.62 a
<i>Humulus scandens</i>	Tender leaf tips	3.01 ± 0.02 b	4.13 ± 0.34 b	6.46 ± 0.17 a	0.57 ± 0.07 b	14.17 ± 0.40 b	294.97 ± 9.89 a	4.87 ± 0.13 a	12.10 ± 1.53 a
	Flowers	24.85 ± 0.50 a	30.53 ± 0.35 a	6.95 ± 0.38 a	1.14 ± 0.03 a	63.47 ± 0.41 a	220.12 ± 7.85 b	3.08 ± 0.09 b	15.70 ± 0.48 a
<i>Mentha haplocalyx</i>	Tender leaf tips	3.99 ± 0.45 b	17.03 ± 0.83 b	2.84 ± 0.03 a	1.28 ± 0.04 b	25.14 ± 1.09 b	200.75 ± 5.83 a	0	9.66 ± 0.06 a
	Flowers	44.11 ± 3.80 a	25.37 ± 1.66 a	3.42 ± 0.20 a	2.24 ± 0.06 a	75.13 ± 5.63 a	101.54 ± 2.13 b	1.55 ± 0.14	6.17 ± 0.18 b
<i>Ocimum basilicum</i>	Tender leaf tips	8.15 ± 0.20 b	7.90 ± 0.18 b	4.42 ± 0.14 b	0.35 ± 0.01 b	20.82 ± 0.17 b	213.57 ± 3.84 a	0	9.68 ± 0.03 a
	Flowers	31.31 ± 0.14 a	23.06 ± 0.13 a	24.09 ± 0.29 a	1.06 ± 0.02 a	79.52 ± 0.50 a	175.77 ± 3.83 b	4.56 ± 0.19	7.49 ± 0.21 b
<i>Schizonepeta tenuifolia</i>	Tender leaf tips	4.70 ± 0.48 b	8.99 ± 0.78 b	2.13 ± 0.08 a	1.46 ± 0.09 b	17.28 ± 1.29 b	295.81 ± 1.97 a	0	11.47 ± 0.73 a
	Flowers	42.33 ± 2.40 a	25.78 ± 2.29 a	2.65 ± 0.13 a	4.09 ± 0.16 a	74.85 ± 4.57 a	88.49 ± 3.09 b	2.43 ± 0.01	6.95 ± 0.23 b

555Means (± SE) followed by different letters illustrate significant differences between flowers and tender leaf tips within each plant species ($P < 0.05$).

556**Table 4. Effect of tender leaf tips with and without sucrose on nymphal survival, development, and *Apolygus lucorum* adult weight**

Host plants	Treatments	Survival rate (%)	Developmental duration (days)		Sex ratio (female/female+male)	Weight (mg)	
			Female	Male		Female	Male
<i>Agastache rugosus</i>	Tender leaf tips	17.50 ± 2.10 b	23.17 ± 0.64 a	23.11 ± 0.70 a	0.57 (12/21)	1.51 ± 0.03 b	1.24 ± 0.05 b
	Tender leaf tips + sucrose	50.00 ± 1.35 a	17.64 ± 0.33 b	17.16 ± 0.33 b	0.47 (28/60)	1.96 ± 0.08 a	1.74 ± 0.05 a
<i>Artemisia argyi</i>	Tender leaf tips	40.83 ± 2.10 b	15.79 ± 0.40 a	15.28 ± 0.36 a	0.49 (24/49)	1.94 ± 0.10 b	1.42 ± 0.08 b
	Tender leaf tips + sucrose	82.50 ± 3.16 a	15.19 ± 0.13 a	15.20 ± 0.12 a	0.54 (53/99)	3.11 ± 0.06 a	2.83 ± 0.07 a
<i>Artemisia lavandulaefolia</i>	Tender leaf tips	44.17 ± 2.85 b	15.62 ± 0.23 a	14.93 ± 0.25 a	0.49 (26/53)	2.91 ± 0.10 b	2.59 ± 0.13 b
	Tender leaf tips + sucrose	64.17 ± 2.50 a	15.18 ± 0.12 a	15.18 ± 0.09 a	0.49 (38/77)	3.27 ± 0.04 a	2.89 ± 0.04 a
<i>Cannabis sativa</i>	Tender leaf tips	17.50 ± 1.60 b	15.00 ± 0.21 a	15.00 ± 0.24 a	0.57 (12/21)	1.98 ± 0.13 b	1.46 ± 0.05 b
	Tender leaf tips + sucrose	49.17 ± 3.44 a	14.21 ± 0.17 b	13.94 ± 0.25 b	0.47 (28/59)	3.29 ± 0.07 a	2.79 ± 0.07 a
<i>Humulus scandens</i>	Tender leaf tips	59.17 ± 2.50 b	14.74 ± 0.24 a	14.38 ± 0.21 a	0.48 (34/71)	2.79 ± 0.08 b	2.28 ± 0.09 b
	Tender leaf tips + sucrose	73.33 ± 1.36 a	14.55 ± 0.13 a	14.71 ± 0.12 a	0.53 (47/88)	3.47 ± 0.06 a	2.75 ± 0.06 a
<i>Mentha haplocalyx</i>	Tender leaf tips	13.33 ± 2.36 b	18.25 ± 0.37 a	17.13 ± 0.40 a	0.50 (8/16)	1.69 ± 0.07 b	1.63 ± 0.11 b
	Tender leaf tips + sucrose	42.50 ± 3.71 a	17.16 ± 0.24 b	16.19 ± 0.20 b	0.49 (25/51)	2.69 ± 0.04 a	2.61 ± 0.06 a
<i>Ocimum basilicum</i>	Tender leaf tips	27.50 ± 1.60 b	16.25 ± 0.38 a	16.65 ± 0.36 a	0.48 (16/33)	2.08 ± 0.08 b	1.55 ± 0.09 b
	Tender leaf tips + sucrose	65.83 ± 4.17 a	15.40 ± 0.13 b	14.95 ± 0.12 b	0.51 (40/79)	3.33 ± 0.07 a	2.89 ± 0.08 a
<i>Schizonepeta tenuifolia</i>	Tender leaf tips	32.50 ± 1.60 b	17.80 ± 0.37 a	16.95 ± 0.43 a	0.51 (20/39)	2.35 ± 0.07 b	2.02 ± 0.08 b
	Tender leaf tips + sucrose	45.83 ± 1.60 a	16.66 ± 0.24 b	17.04 ± 0.22 a	0.53 (29/55)	3.13 ± 0.07 a	2.63 ± 0.07 a

557Means (± SE) followed by different letters illustrate significant differences between different treatments within each plant species ($P < 0.05$).

Figure 1. Numbers (mean $\pm$ SE) of eggs laid by female *Apolygus lucorum* on host plants in flowering stage and vegetative stage in choice trials enclosed by cages A: *Agastache rugosus*; B: *Artemisia argyi*; C: *Artemisia lavandulaefolia*; D: *Cannabis sativa*; E: *Humulus scandens*; F: *Mentha haplocalyx*; G: *Ocimum basilicum*; H: *Schizonepeta tenuifolia*. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ indicated a significant difference between the vegetative and flowering stages (Paired t-tests).

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