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Host plant-mediated prey preference and consumption by an aphidophagous ladybird, *Menochilus sexmaculatus* (Fabricius) (Coleoptera: Coccinellidae)

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Abstract

The impact of host plant-aphid combination on the prey consumption and prey preference by adult ladybird, *Menochilus sexmaculatus* (Fabricius) (Coleoptera: Coccinellidae) was studied, using aphid-prey, *Aphis craccivora* (Koch) and *Lipaphis erysimi* (Kalt.), in the laboratory. Monotypic aphids, *A. craccivora*, raised separately on Indian bean, *Dolichos lablab* L., and poison buttercup, *Ranunculus sceleratus* L., and *L. erysimi* cultured on radish, *Raphanus sativus* L., and mustard, *Brassica campestris* L., were provided. Adult male and female ladybirds consumed significantly greater number of *A. craccivora* infested on *D. lablab* than those on *R. sceleratus*. Similarly, they consumed a greater number of *L. erysimi* raised on *R. sativus* than those on *B. campestris*. The results indicated that host plant allelochemicals/toxicants had a direct effect on the palatability and prey consumption, as the ladybird treated the same aphids differently that was raised on different hosts. Prey preference, using a choice condition, was tested by providing both the aphid species raised on toxic hosts in a common microcosm. Both adult male and female of *M. sexmaculatus* preferably consumed the aphid, *A. craccivora*-infested *R. sceleratus* over *L. erysimi*-infested *B. campestris* in all diet treatments. The preference indices (β and C) further skewed the results towards *A. craccivora*, which suggest that ladybirds preferred *A. craccivora* on encountering aphids raised on toxic hosts. It could be concluded that dietary selection in ladybirds depends largely on the aphid–host combination, and a suitable host may aid the augmentative rearing of both aphids and ladybirds.

Keywords: Aphids, *Aphis craccivora*, *Brassica*, *Menochilus sexmaculatus*, Diet, *Lipaphis erysimi*

Background

Majority of ladybirds (Coleoptera: Coccinellidae) are important predators and biocontrol agents of numerous phytophagous pests, viz. aphids, scale insects, mealy bugs, thrips, mites, and whiteflies (Omkar and Pervez 2004, 2016; Hodek et al. 2012). A thorough understanding of ladybirds' dietary habits can help in maximizing their biocontrol potential (Michaud 2005; Provost et al. 2006; Sloggett 2008a, b; Hodek and Evans 2012; Pervez et al. 2018). However, diet suitability in aphidophagous ladybirds seems unpredictable, as the same aphid can be both toxic and nutritious (Guroo et al. 2017). For instance, earlier reports considered black bean aphid, *Aphis craccivora* (Koch), as unsuitable food for ladybirds (Hodek 1996), due to the presence of toxic allelochemicals, viz. amines canavanine and ethanolamine (Obatake and Suzuki 1985). Ferrer et al. (2008) considered it as a sub-optimal prey, as the larvae feeding on it grew into lighter adults with decreased ovarioles number. On the contrary, recent findings suggested it to be highly nutritious after being raised on Indian bean, *Dolichos lablab* L. (=*Lablab purpureus* L.), and recommended it as the most suitable prey for mass rearing of certain aphidophagous ladybirds (Omkar and Mishra 2005; Chaudhary et al. 2016).

Host plant seems to have a direct influence on prey preference and prey suitability in ladybirds (Ferrer et al. 2008; Giorgi et al. 2009). Apart from nutrition, certain host plants provide an ecological refuge to the aphids by

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chemically protecting them from their natural enemies (Chaplin-Kramer et al. 2011). Toxic plant allelochemicals deteriorate the aphid quality and make them unsuitable for predators (Pratt 2008). However, continuous rearing of aphidophagous ladybirds on toxic prey for generations enables the offspring to easily thrive on the toxic prey than the nutritious ones (Rana et al. 2002). Mixing toxic aphids with nutritious ones perhaps compliments the nutrient-deficiency of the former and cumulatively enhances the fitness of ladybirds (Nedved and Salvucci 2008; Guroo et al. 2017). Mustard aphid, *Lipaphis erysimi* (Kaltenbach), infesting *Brassica campestris* L. is known to decrease the fitness of certain ladybirds (Omkar and Mishra 2005), as it sequesters toxic allelochemicals from the host plant (Ahuja et al. 2010).

Zig-zag ladybird, *Menochilus sexmaculatus* [=*Cheilomenes sexmaculata*] (Fabricius) preferably feeds on *A. craccivora* infesting Indian bean, *D. lablab* L. (=*Lablab purpureus* L.) (Omkar and Bind 1998) and thereby optimizes its fitness (Omkar and Bind 2004). It is an oriental ladybird having a wide prey range (Saleem et al. 2014). Its immature stages can easily be reared on mustard aphid, *L. erysimi*; however, the fecundity and developmental rate were not very boosting (Singh et al., 2008).

Owing to its high abundance of *M. sexmaculatus* in the agricultural fields of North India, we considered it as a model to determine the ladybird behavior towards aphids cultured on different host plants. The objective of the present investigation was to better understand the status of *A. craccivora* in terms of prey preference and prey suitability to ladybirds. Also, the difference in the prey consumption, when ladybirds fed on monotypic aphids or mixed aphids, was investigated.

Materials and methods

Stock maintenance

Adults of *M. sexmaculatus* were collected from the agricultural fields of Kashipur, Uttarakhand, India (30.2937° N, 79.5603° E) and brought to the laboratory. These were sexually identified by a careful examination of lower abdominal segments with the help of Trinocular Assembly (Lyzer IS0-9001: magnification × 40) connected to a computer. Thereafter, we paired in Petri dishes (2.0 × 9.0 cm diameter) containing sufficient quantity of monotypic aphids, *A. craccivora* on pieces of leaves/twigs of *D. lablab* and *Ranunculus sceleratus*, respectively, and *L. erysimi* infested on *Raphanus sativus* and *B. campestris*, respectively ($n = 10$), and kept in the Environmental Test Chamber (REMI Instruments, India) at controlled conditions (25 ± 1 °C, 65 ± 5% R.H and 12L: 12D). The F_1 eggs laid by the female ladybird from each host plant–aphid combinations were reared on the same host plant–aphid combination till adult emergence. The newly emerged F_1 adults were sexually identified and isolated in separate Petri dishes (2.0 × 9.0 cm and prey as above) for experiments.

Response to single aphid–host combination

Twelve-hour starved 10-day-old virgin adult male *M. sexmaculatus* were kept singly in a glass beaker (11.0 cm height and 8.5 cm diameter) containing 100 third instars of aphids (i) *A. craccivora* infested on twigs of *D. lablab*, (ii.) *A. craccivora* on twigs of *R. sceleratus* (iii) *L. erysimi* on twigs of *R. sativus*, and (iv) *L. erysimi* on twigs of *B. campestris*. The beakers were covered by a muslin cloth fastened with rubber bands. The beakers were kept in the environmental test chamber (ETC) (REMI Instruments, India) maintained at above abiotic conditions. After 12 h, the beakers were removed and counted the live aphids to quantify the number of aphids consumed. The experiment was repeated using adult female *M. sexmaculatus*. The experiment was replicated ten times. The data on prey consumption were tested for normality, using Kolmogorov–Smirnoff Test and homogeneity of variance, using Bartlett's Test using statistical software, SAS 9.0 (2002). The data were subjected on number of aphid consumed to one-way ANOVA and compared the means using Tukey's HSD test using SAS 9.0 (2002). Thereafter, the data were subjected on aphids, raised on different host plants and consumed by the two sexes of *M. sexmaculatus* to Factorial ANOVA using "aphid species," "host plant," and "gender" as independent variables and "prey consumed" as dependent variable using SAS 9.0 (2002).

Prey preference

Prey preference was determined by offering mix-aphids cultured on toxic host plants to the adult male and female *M. sexmaculatus* in a bid to find out the preferred aphid–host combination. For the purpose, the aphids, *A. craccivora (Ac)* cultured on *R. sceleratus* and *L. erysimi (Le)* cultured on *B. campestris*, were offered to the adult male and female *M. sexmaculatus* in three ratios, i.e., *Ac* to *Le* 50:100, 75:75, and 100:50. For the purpose, a single 12-h starved ten-day-old adult male ladybird was kept in a glass beaker (11.0 cm height and 8.5 cm diameter), containing mix proportion of (i) 50 *Ac* and 100 *Le*, (ii) 75 *Ac*, and 75 *Le*, and (iii) 100 *Ac* and 50 *Le* infested on respective toxic host plant twigs. The beaker (as above) was covered and kept in the ETC (conditions as above). After 24 h, the beaker was removed and quantified for the number of aphids consumed (as above). The experiment was repeated, using an adult female of *M. sexmaculatus* as the predator. The entire experiment was replicated ten times.

Manly's preference index (Manly 1972) using formula, $\beta = \log (N_A/r_A)/[\log (N_A/r_A) + \log (N_B/r_B)]$ for each treatment, where N_A and N_B are number of aphids A and B offered to the adult predator and r_A and r_B are unconsumed aphids. Manly's preference index removes prey depletion error, i.e., it is applicable in those experiments, where killed prey items are not replaced (Cook 1978; Sherratt and Harvey 1993). Adult ladybird prefers aphid A if β is close to 1, and aphid B is preferred if β is close to 0. Index value close to 0.5 revealed no preference. β for significant difference from a value of 0.5 was tested, using one sample *t* test in each treatment (SAS 9.0). Prey preference was also determined by C index (i.e., $C = (E_A \times N_B)/(E_B \times N_A)$, where E_A and E_B are the number of aphids A and B consumed. C index above 1.0 indicates the preference for aphid A, while below 1.0 indicates the preference for aphid B (Sherratt and Harvey 1993). C index in each treatment was subjected to one sample *t* test for significant difference from a value of 1.0. The data on number of aphid consumed were subjected to Wilcoxon's matched-pair signed rank test (SAS Version 9.0). The proportions of the two aphids consumed by the adults *M. sexmaculatus* were subjected to two-way ANOVA using "aphid species" and "gender" as independent variables and "proportion of prey consumed" as a dependent variable (SAS 9.0, 2002).

Results and discussion

Both adult male ($F = 25.86$; $P < 0.0001$; df = 3, 39) and female ($F = 45.51$; $P < 0.0001$; df = 3, 39) of *M. sexmaculatus* consumed significantly greater number of aphids, *A. craccivora* infested on *D. lablab*, followed by *L. erysimi* infested on *R. sativus* (Fig. 1). This revealed that *A. craccivora* cultured on *D. lablab* was the best aphid–host combination culminating in maximum prey consumption. Seemingly, the biochemical contents of *D. lablab*, like sugars, alcohols, and essential oils (Al-Snafi 2017) made *A. craccivora* to be highly palatable to *M. sexmaculatus*, resulting in its high consumption. This aphid also infests other hosts, viz. cowpea, glyricidia, and groundnut, which are frequently visited by the ladybirds (Jaba et al. 2010).

The aphids, *A. craccivora* and *L. erysimi*, reared on *R. sceleratus* and *Brevicoryne brassicae*, respectively, were consumed lesser by the two sexes of the ladybirds with insignificant difference between their means (Tukey's range = 3.81; Fig. 1). It seems that *A. craccivora* infesting *R. sceleratus* were less palatable to *M. sexmaculatus*. *Ranunculus* sp. are known to be rich in toxic secondary metabolites, such as di and tri terpenes, glycosides, steroids, coumarins, phenolic compounds, and flavonoid contents, which may account for the lesser consumption of its herbivore (Hachelaf et al. 2013; Pervez and Kumar 2017). *A. craccivora* exploits this plant as a host in the months of June to August in North India during the absence of its regular host. Hence, *R. sceleratus* has an ecological significance in terms of providing refuge to *A. craccivora* along with retaining the ladybirds, particularly *M. sexmaculatus*, during the absence of other host agricultural crops. It is evident from obtained results that palatability and consumption of *A. craccivora* were largely dependent on the host plant rather than its own nutrients. This explains the disparity in the reports by various authors about its suitability to different ladybirds (Omkar and Bind 2004; Omkar and Mishra 2005; Chaudhary et al. 2016).

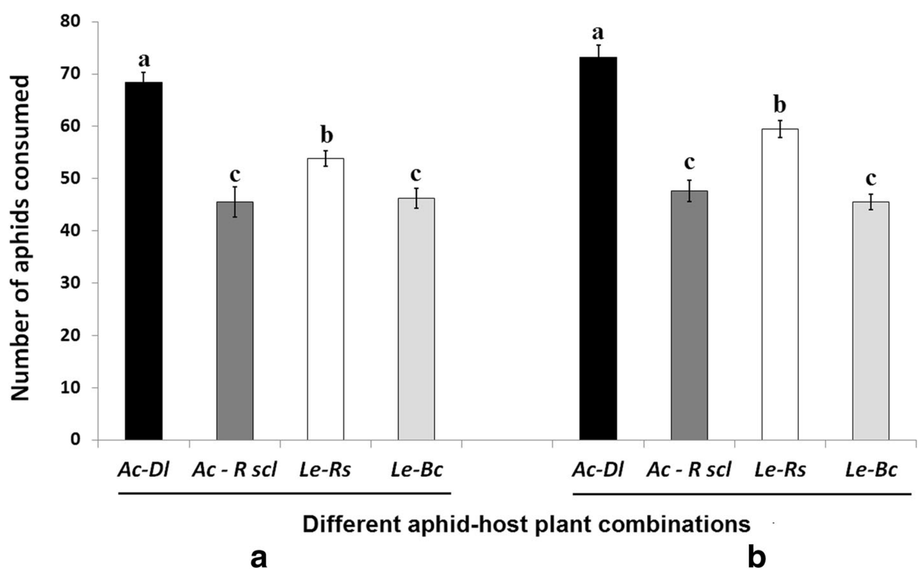

Fig. 1 Number of aphids consumed by adult **a** male and **b** female of *M. sexmaculatus* when fed on different aphid–host plant combinations (i.e., (i) *Ac-Dl* = *A. craccivora–D. lablab*, (ii) *Ac-R scl* = *A. craccivora–R. sceleratus*, (iii) *Le–Rs* = *L. erysimi–R. sativus*, and (iv) *Le–Bc* = *L. erysimi–B. campestris*. Error bars denote standard deviation. Bars indicated by the same letter are not statistically different at $P < 0.05$ (Tukey's test)

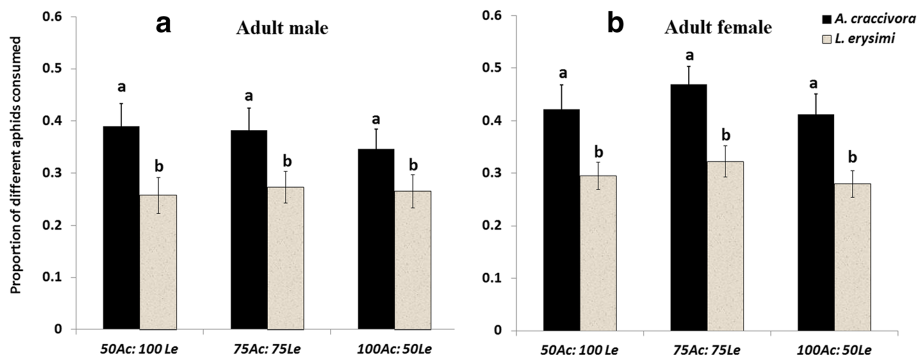

Fig. 2 Proportions of aphid species [*A. craccivora (Ac)* and *L. erysimi (Le)* reared on *R. sceleratus* and *B. campestris*, respectively] consumed by adult **a** male and **b** female of *M. sexmaculatus* when the aphids were provided in different ratios. Error bars show standard error. Bars indicated by the same letter are not statistically different at $P < 0.05$ (Tukey's test)

Adults *M. sexmaculatus* consumed greater number of *L. erysimi* raised on *R. sativus* than those raised on *B. campestris*. *Brassica* plants, particularly *B. campestris*, have a strong defense system and contain allelochemicals, like glucosinolates, isothiocyanates, nitriles, and phytoalexins (Ahuja et al. 2010). *L. erysimi* sequesters these allelochemicals, which reduce its palatability to its predators. These chemicals also are lower in their nutritive value and thereby negatively affecting the development and fecundity of its predators (Omkar and Mishra 2005). From ladybirds' perspective, *D. lablab* and *R. sativus* are considered as better hosts for the biocontrol of *A. craccivora* and *L. erysimi*, respectively. Two-way ANOVA reveals significantly main effects of "aphid species" ($F = 43.29$; $P < 0.0001$; df = 1) and "gender" ($F = 9.81$; $P = 0.003$; df = 1). The interaction "aphid species" × "gender," however, was not statistically significant ($F = 1.54$; $P = 0.223$; df = 1, 39). The significant main effect of sex on the aphid consumption was due to the difference in the quantitative aphid consumption, as females consumed a greater number of aphids in all aphid–host combinations. This is largely attributed to the size disparity in adults, as females are larger than the males.

The two inferior aphid–host combinations in terms of lesser consumption were used in the prey-preference experiment. Adult male *M. sexmaculatus* significantly preferred aphid *A. craccivora* over *L. erysimi* raised on toxic host plants in all three mixed aphid–diet combinations, i.e., at 50:100 (*Ac* to *Le*) ratio ($Z_{(1,\ 18)} = -3.7968$; $P = 0.0001$), 75:75 (*Ac* to *Le*) ratio ($Z_{(1,\ 18)} = -3.7968$; $P = 0.0001$), and 100:50 (*Ac* to *Le*) ratio ($Z_{(1,\ 18)} = 2.3240$; $P = 0.0210$; Fig. 2a). Similarly, adult female ladybird preferably consumed *A. craccivora* in the three diet treatments (i.e., at 50 *Ac*:100 *Le*; $Z_{(1,\ 18)} = -3.753$; $P = 0.0002$), 75 *Ac*:75 *Le*; $Z_{(1,\ 18)} = -2.4633$; $P = 0.0138$), and 100 *Ac*:50 *Le*; $Z_{(1,\ 18)} = 3.1917$; $P = 0.0014$, see Fig. 2b). On the contrary, ladybird, *Propylea dissecta* (Mulsant), preferred *L. erysimi* when provided with the same aphid combinations (Pervez and Kumar 2017).

The factorial ANOVA revealed the data on number of aphid consumed to be statistically significant ($F = 30.36$; $P < 0.0001$; df = 1). There were significant main effects of "host" ($F = 154.95$; $P < 0.0001$; df = 1), "aphid species" ($F = 27.55$; $P < 0.0001$; df = 1), and "gender" ($F = 4.38$; $P < 0.05$; df = 1) on the number of prey consumed (Table 1). This clearly indicates that these independent variables had a major effect on the aphid consumption. The interaction between "aphid species" and "host" was also significant ($F = 22.58$; $P < 0.0001$; df = 1). However, the interactions between "gender" and "aphid species" ($F = 0.13$; $P = 0.7239$; df = 1), "gender" and "host" ($F = 2.55$; $P = 0.\ 1149$; df = 1), and "aphid species" × "host" × "gender" ($F = 0.41$; $P = 0.5253$; df = 1) were insignificant. Preference indices, viz. β and C had significant t values in all the combinations (Table 2), which further corroborates the inference that *M. sexmaculatus* preferred *A. craccivora* over *L. erysimi* despite the former prey being raised on

Table 1 Details of three-way factorial ANOVA using "gender," "host plant," and "aphid species" as independent variables

Source	df	Mean square	F value	*P* value
Gender	1	174.05	4.38	$P < 0.05$
Host plant	1	6160.05	154.95	$P < 0.0001$
Aphid species	1	1095.20	27.55	$P < 0.0001$
Gender × host plant	1	101.25	2.55	$P = 0.1149$
Gender × aphid species	1	5.000	0.13	$P = 0.7239$
Host plant × aphid species	1	897.8	22.58	$P < 0.0001$
Gender × host plant × aphid species	1	16.20	0.41	$P = 0.5253$

Tukey's range = 2.81929
df = 1

Table 2 Preference indices (β and C) evaluated from different aphid proportions (*Acraccivora*: *L. erysimi*) exposed to *M. sexmaculatus* in cafeteria experiment

Predator	Aphid ratio	β index	*t* value	*C* index	*t* value
Adult male *M. sexmaculatus*	50:100	0.700 ± 0.06	$t = 5.54$; $P < 0.01$	1.851 ± 0.39	$t = 7.16$; $P < 0.01$
	75:75	0.783 ± 0.05	$t = 5.58$; $P < 0.01$	1.515 ± 0.25	$t = 6.03$; $P < 0.01$
	100:50	0.716 ± 0.06	$t = 6.25$; $P < 0.01$	1.967 ± 0.78	$t = 8.25$; $P < 0.01$
Adult female *M. sexmaculatus*	50:100	0.670 ± 0.06	$t = 2.14$; $P < 0.05$	1.539 ± 0.33	$t = 2.62$; $P < 0.05$
	75:75	0.615 ± 0.04	$t = 2.84$; $P < 0.05$	1.596 ± 0.20	$t = 2.89$ $P < 0.05$
	100:50	0.565 ± 0.03	$t = 2.41$; $P < 0.05$	1.498 ± 0.22	$t = 2.54$; $P < 0.05$

Ladybird prefers *A. craccivora* if β is close to 1 and *L. erysimi* if β is close to 0. Similarly, *A. craccivora* is preferred if the *C* index is more than 1 and *L. erysimi* is preferred if the *C* index is less than 1

toxic host. However, in a similar experiment, larvae and adults of ladybird, *Coccinella septempunctata* L. prefer to consume *L. erysimi* over the aphid, *Brevicoryne brassicae* L. with significantly high values of β and *C* preference indices (Guroo et al. 2017).

Conclusions

It could be concluded that: (i) host plant affected the aphid palatability to the ladybird, which explains the contrary reports of suitability about *A. craccivora* to its predatory ladybird, (ii) *D. lablab* was a better host to raise palatable *A. craccivora* to *M. sexmaculatus* than *R. sceleratus*, (iii) similarly, *R. sativus* was better than *B. campestris* to culture *L. erysimi*, and (iv) *M. sexmaculatus* preferred *A. craccivora* over *L. erysimi*-infested toxic hosts in choice condition. Obtained results also explain the strong affinity of *M. sexmaculatus* with *A. craccivora*, as this predator is more witnessed in the vicinity of *A. craccivora*, regardless of the host plants.

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Authors' contributions
AP has planned the outline of this research and designed the methodology. He did all the analyses and drafted the manuscript. SC assisted him in maintaining laboratory culture and performing experiments. Both the authors read and approved the final manuscript.

Ethics approval and consent to participate
Not applicable

Consent for publication
Not applicable

Competing interests
Both authors declare that they have no competing interests.

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