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Reproduction and demography of an Aphidophagous ladybird, Hippodamia variegata on six aphid species

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Abstract

We tested six aphid species, viz. *Aphis gossypii, Aphis craccivora, Brevicoryne brassicae, Lipaphis erysimi, Myzus persicae* and *Uroleucon compositae* as essential foods needed for the reproduction and demography of an aphidophagous ladybird, *Hippodamia variegata.* Females were highly fecund (1210.8 ± 55.31 eggs) with prolonged oviposition period (56.30 ± 2.36 days) and laying most viable eggs ($92.91 \pm 0.81\%$) when fed on *A. gossypii* (reared on *Lagenaria vulgaris*) with the highest net reproductive rate (449.45 ± 20.53 females / female). *Aphis craccivora* (raised on *Dolichos lablab*) supported optimal value for intrinsic rate of increase (0.183 ± 0.003) with the shortest generation time (32.40 ± 0.557 days). Other diets didn't show improved performance but quantified as essential foods. *Brassica* hosted *B. brassicae* and *L. erysimi* were less suitable but not the rejected prey. Age-specific fecundity of female *H. variegata* was triangular in function with peak oviposition during her early reproductive age when fed on *B. brassicae* or *L. erysimi*. Fecundity was positively correlated with egg-viability and oviposition period. We used jackknife technique to estimate and compare the demographic parameters within the groups. High values of intrinsic and finite rates of increase on *A. gossypii* and *A. craccivora* affirm their suitability for augmentative rearing of *H. variegata*. We conclude that both *A. gossypii* and *A. craccivora* on above respective host-plants are highly suitable aphid-diets for mass-multiplication of *H. variegata*.

Keywords Hippodamia variegata · Coccinellidae · Aphis gossypii · Demography · Aphids · Prey

Introduction

Predaceous ladybirds (Coleoptera: Coccinellidae) are important biocontrol agents of numerous phytophagous insectpests, especially aphids (Dixon 2000; Hodek et al. 2012; Omkar and Pervez A. 2016). Their dietary habits have been extensively investigated by many workers (Evans and

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Gunther 2005; Honek et al. 2008a, 2008b; Sloggett 2008a, 2008b; Hodek and Evans 2012). Their accepted foods (Hodek and Evans 2012) are classified as essential (supporting development and reproduction of species) and alternative (that supports only the survival of species) food. Factors, such as aphid-plant interactions (Jalali and Michaud 2012), prey body size (Sloggett 2008b), prey nutritive value (Lundgren 2009; de Lima et al. 2018), etc. play major roles in the ladybirds' prey suitability. Prey gradually becomes more suitable to ladybirds if they are reared for many generations on the former (Rana et al. 2002). Further, the mixing of two prey-species of varied suitability could be better than single suitable preyspecies as ladybirds' diets (Soares et al. 2004; Ferrer et al. 2008; Nedved and Salvucci 2008); however, sometimes mixed diet fails (Mehrparvar et al. 2013). Certain factitious prey and artificial diets support cost-effective mass-rearing of predaceous ladybirds for successive generations (Sun et al. 2017; Cheng et al. 2018). However, success related to massmultiplication of the ladybirds can be best described by demographic studies (Yu et al. 2013; Papanikolaou et al. 2014).

Aphidophagous ladybirds primarily feed on aphids; however, the suitability of the latter depends largely on host-plants (Francis et al. 2000; Rakhshan and Ahmad, M.E. 2013). For instance, Hodek and Evans (2012) listed aphid, Aphis craccivora (Koch) as toxic and low quality prey, as larvae of ladybird, Harmonia axyridis (Pallas) did not develop and the adults died when fed on A. craccivora infested on Robinia pseudoacacia L. (Hukusima and Kamei 1970) and Vicia faba L. (Okamoto 1966). Here, aphid-quality was largely ascribed to toxic allelochemicals, amines canavanine and ethanolamine present in both aphid and hosts (Obatake and Suzuki 1985). Contrarily, a few ladybirds preferred A. craccivora (reared on Dolichos lablab L.) and found it highly nutritious for reproduction (Pervez and Omkar 2004a; Omkar and Mishra G. 2005). Similarly, waxy cabbage aphid, Brevicoryne brassicae L. (reared on Brassica oleracea L.) was listed as rejected prey (Hodek and Evans 2012), as it sequesters highly toxic allelochemicals, viz. glucosinolates from the host plant, Brassica sp., which shielded them against predators (Pratt 2008; Kos et al. 2011, 2012).

Hippodamia variegata (Goeze) is a Palaearctic, eurytopic, aphidophagous ladybird occurring in aphid prevalent agroecosystems of North India and one that has tremendous aphid biocontrol potential (Pervez and Maurice 2011; Pervez and Singh 2013). It has been established successfully in the USA, Canada (Krafsur et al. 1996; Wheeler Jr. and Stoops 1996), Bulgaria (Natskova 1973), Ukraine (Gumovskaya 1985), and Italy (Nicoli et al. 1995). Information on its prey and food association is a prerequisite for its augmentation and biocontrol prospects. Adults and fourth instars of H. variegata have immense biocontrol potential against aphid, Aphis gossypii (Glover) (Pervez, and Pooja and Bozdogan, H. 2018). A few authors investigated the biology and life parameters of this ladybird on aphids, Myzus persicae (Sulzer) (Lanzoni et al. 2004), A. gossypii (Wu et al. 2010) and Aphis fabae Scopoli (Jafari 2011). Recently, bootstrap technique was used to determine age-stage two-sex life-table of H. variegata on Russian wheat aphids, Diuraphis noxia (Kurdjumov) (Zanganeh et al. 2015) and Sitobion avenae Fabricius (Moghaddam et al. 2016). However, an alternative jackknife method may better analyze these studies, as it calculates pseudo-values of each life-table parameter (Maia et al. 2000). Modification of this method enabled us to perform Fanalysis of each life-table parameter and to fit jackknife derived pseudo-values to the polynomial regression models (Maia et al. 2014). Previously cited demographic studies on H. variegata focussed on single aphid species, and a comparative study at the aphid level is lacking. Hence, the laboratory study was designed to (i) determine the reproduction and demography of H. variegata on six aphids, viz. A. craccivora, A. gossypii, B. brassicae, Lipaphis erysimi (Kalt.), M. persicae and Uroleucon compositae (Theobald), (ii) compare the preyspecific demographic values of each parameter using our modified jack-knife method and, (iii) compare our data on prey-species from the literature to determine its suitability to ladybirds.

Materials and methods

Collecting and rearing of *H. variegata* and aphid species

We collected adults of *H. variegata* from the suburbs of Uttarakhand, Northern India (30.2937°N, 79.5603°E) and brought them to the laboratory. They were sexed and paired in a Petri dish $(2.0 \times 9.0 \text{ cm}^2)$ containing ad libitum A. gossypii infested on pieces of leaves of Lagenaria vulgaris L. (bottle gourd). Similarly, adult ladybirds were paired in Petri dishes containing monotypic aphids, A. craccivora, B. brassicae, L. erysimi, M. persicae and U. compositae infested on twigs of D. lablab (Fabaceae), B. oleracea (Brassicaceae), Brassicae campestris Linnaeus (Brassicaceae), Solanum nigrum Linnaeus (Solanaceae) and Carthamus tinctorius Linnaeus (Compositae), respectively (n = 10). We cultured these host-plants in our college campus crop-field behind our research laboratory and inoculated them with respective aphids. The Petri dishes containing respective aphids-infested on host plants twigs and a pair of adult ladybirds were kept in the Environmental Test Chamber (*REMI Instruments*, India) at controlled conditions $(27 \pm$ $1 \degree C$, $65 \pm 5\%$ R.H and 12 L: 12D). A preliminary experiment revealed that H. variegata reproduced best at 12 L: 12D photoperiod (Pervez, unpublished data). Maia et al. (2014) found its optimal demographic values and fittest generation at 27 °C. We observed mating pairs for daily oviposition and transferred the eggs laid to new Petri dishes (size as above). On hatching, we transferred the neonates to muslin covered beakers (10.5 \times 15 cm^2) and provided them with daily replenished supply of ad libitum same aphid-diet, which was given to their parents, until the larval stages were completed. We sexed the emerging F₁ adults and paired them in Petri dishes (prey and size as above) to obtain F₂ generation eggs for further experimentation.

Reproduction and demographic analysis on six aphid species

We reared hundred first instars of *H. variegata*, obtained from F_2 generation eggs, on daily replenishment ad libitum supply of *A. gossypii* infested twigs of *Lagenaria vulgaris* in the glass beakers (9.0 × 11.0 cm²). To avoid overcrowding, we kept only 10 first instars in one beaker, (as it is equivalent to a single minor egg-cluster and the larvae are small sized) and thus used ten beakers for hundred instars. We replenished the diet along with host plant daily and monitored the instars for

survival and moulting until pupation. The adults, emerged out after pupation, were sexed and kept in isolation in separate Petri dishes, i.e. a single adult per Petri dish $(2.0 \times 9.0 \text{ cm}^2)$ on the same aphid-diet (aphid and host as above). The sexratio in terms of female proportion of eclosed adults was recorded. Ten-day-old virgin adult male and female, *H. variegata* were paired in a Petri dish (size and prey as above) (n = 10). This pair was kept together for lifetime until the adult female died. Simultaneously, we recorded daily oviposition, fecundity and percent egg viability. We repeated the same experiment using the remaining five aphid species on their respective host plants.

Estimation of demographic parameters and statistical analyses

We tested the data on reproductive parameters, viz. fecundity, percent egg viability and oviposition period, of *H. variegata* on different diets for normality using Kolmogorov – Smirnoff Test and homogeneity of variance using Bartlett's Test on statistical software, SAS 9.0. Thus, after checking normality and homoscedasticity assumptions, the data were subjected to one way ANOVA, and means were compared using Tukey's Test on SAS 9.0. We correlated fecundity with percent egg viability and oviposition period using Pearson's correlation on SAS (Version 9.0).

The estimates for each demographic parameter, viz. net reproductive rate (Ro), intrinsic rate of increase (rm), finite rate of increase (λ), generation time (T_c) and Doubling Time (DT) for each aphid-diet treatment was obtained by following Maia et al. (2000) and further computational advances following Maia et al. (2014) using the statistical software, R (R Development Core Team. 2010). Maia et al. (2014) modified the procedure for evaluating the r_m estimates by using the uniroot function, based on Brent's iterative method (Brent 1973) in the R program (R Development Core Team. 2010). This procedure improved the initial iterative methods to estimate r_m-values and subsequently other derived demographic parametric values, viz. T_c , D.T., and λ (Maia et al. 2000). The pseudo-values for each demographic parameter were also evaluated using jackknife method (for details, see Maia et al. 2000, 2014). The evaluation of pseudo-values helped us to obtain means, standard errors and F-values for each parameter estimated in each group. The box-and-whiskers-plots were constructed to illustrate the dispersion of pseudo-values within each group, which is directly related to the uncertainty of their estimates.

Results

Hippodamia variegata reproduced on all the six aphid-diet treatments. The diets significantly affected the reproductive

attributes in terms of fecundity (F = 47.20; P < 0.0001; d.f. = 5, 54), percent egg viability (F = 162.87; P < 0.0001; d.f. = 5, 54) and the duration of oviposition (F = 18.80; P < 0.0001; d.f. = 5, 54) (Table 1). Females were most fecund (1210.8 ± 55.31 eggs) when fed on *A. gossypii* with an individual laying 1469 eggs, while minimum (639.8 ± 14.70 eggs) eggs when fed on *L. erysimi* (Table 1). The percent egg viability was maximum on *A. gossypii* (92.91 ± 0.81) and minimum when *L. erysimi* (52.76 ± 1.70) was used as prey. Similarly, the female *H. variegata* oviposited for the longest duration when fed on *L. erysimi* (33.00 ± 1.09 days). The prey suitability rank in terms of fecundity was: *A. gossypii* > *A. craccivora* > *U. compositae* > *M. persicae* > *B. brassicae* > *L. erysimi*.

The temporal pattern of fecundity showed a triangular shape (Fig. 1) which suggests that daily oviposition increases with the increase in mean reproductive age. We used polynomial regression analysis to explain the relationship between the mean reproductive age and the mean eggs laid when six aphid diets were used. The fourth level of polynomial gave the best fit for aphid diets, viz. A. gossypii $(1E-05X^4 + 0.003X^3 0.206X^2 + 4.8626X - 1.2884$; r = 0.973; P < 0.0001), A. craccivora $(4E-05X^4+0.006X^3-0.341X^2+6.7471-$ 8.2576; r = 0.969; P < 0.0001), U. compositae (3E-05X⁴ + $0.0054X^{3}-0.3117X^{2}+6.3222-6.3571; r = 0.966; P < 0.0001)$ and *M. persicae* $(Y = -5E-05X^4 + 0.0062X^3 - 0.3055X^2 + 0.0062X^3 - 0.006$ 5.6508X - 6.5493; r = 0.965; P < 0.0001). The high values of coefficient of regression (r) indicate that data predicted in these regression lines were statistically significant. Fecundity functions of H. variegata on aphids, A. gossypii, A. craccivora, U. compositae and M. persicae had positive skewness with the peak coming during the early phases of life (Fig. 1a-d). The second Level (Binomial) regression analysis gave the best fit for *B. brassicae* ($-0.0271X^2 + 1.1482X +$ 10.149; r = 0.806; P < 0.001) and L. ervsimi (- 0.0443X² + 1.4816X + 11.13; r = 0.916; P < 0.0001). Fecundity functions of H. variegata when fed on B. brassicae and L. erysimi exhibited negative skewness and the peak of oviposition occurred late in its reproductive phase of life (Fig. 1e-f).

Fecundity was positively correlated with both percent egg viability (r = 0.896; P < 0.05) and oviposition period (r = 0.963; P < 0.01). Similarly, percent egg viability was also positively correlated with the oviposition period (r = 0.9703; P < 0.001). Demographic parameters of *H. variegata* for each diet treatment are presented (Table 2). We recorded a significantly higher net reproductive rate on *A. gossypii* than on other diets. Box and whisker plots of the pseudo-values show that both intrinsic and finite rates of increase of *H. variegata* when fed on *A. gossypii*, *A. craccivora* and *U. compositae* are significantly higher than the other three aphid-diets (Fig. 2). Similarly, mean generation and doubling times of the ladybird were shorter on *A. gossypii*, *A. craccivora* and *U. compositae* (Table 2; Fig. 2).

Aphid species	Fecundity (in eggs)	Egg Viability (in %)	Oviposition period (in days)	
A. gossypii	1210.8 ± 55.31 a (977–1469)	92.91±0.81 a (89.5–97.3)	56.30 ± 2.36 a (47–69)	
A. craccivora	998.0±30.17 b (862–1124)	91.03 ± 0.94 a (86.3–95. 2)	51.90 ± 2.37 a b (39–65)	
U. compositae	1039.2 ± 25.99 b (881–1179)	87.06±0.66 ab (84.3–89.6)	49.00 ± 1.88 b (42–60)	
M. persicae	855.3 ± 11.67 c (780–906)	81.04 ± 1.41 b (74.3–89.6)	46.20 ± 0.93 bc (42–49)	
B. brassicae	771.6±18.18 d (710–852)	76.30±1.10 c (72.3–81.2)	41.60 ± 2.23 c (24–49)	
L. erysimi	639.8 ± 14.70 e (588–719)	52.76 ± 1.70 d (42.3–59.6)	33.00 ± 1.09 d (28–38)	
*F-value	47.20	162.87	18.88	

 Table 1
 Reproductive parameters of H. variegata when six monotypic aphid-diets were provided

Data are Mean \pm S.E

Range of each reproductive parameter has been provided in parentheses

*P < 0.0001; d.f. = 5,54; Tukey's range = 4.18

Different letters mean significance within the distribution

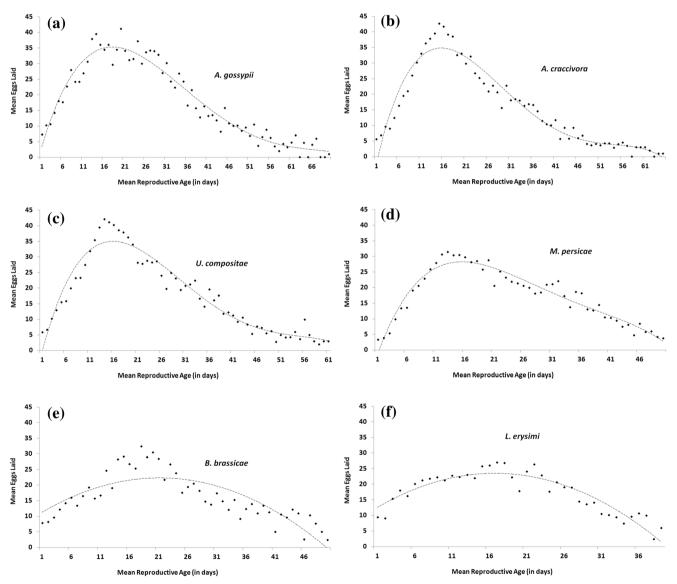


Fig. 1 a-f Mean eggs laid by the female *H. variegata* during her mean reproductive age when fed on monotypic aphid species, viz. a *A. gossypii*, b *A. craccivora*, c *U. compositae*, d *M. persicae*, e *B. brassicae* and f *L. erysimi*

Table 2 Demographic parameters of *H. variegata* when six monotypic aphid diets were provided

Aphid species	Net Reproductive Rate	Intrinsic rate of increase	Finite rate of increase	Mean Generation Time	Doubling Time
A. gossypii	449.45 ± 20.53 a	0.179 ± 0.003 a	1.196 ± 0.004 a	34.12 ± 0.662 c	3.87 ± 0.084 c
A. craccivora	376.61 ± 11.40 b	0.183 ± 0.003 a	1.200 ± 0.003 a	32.40 ± 0.557 c	$3.79 \pm 0.069 \ c$
U. compositae	371.44 ± 9.29 b	0.181 ± 0.003 a	1.199 ± 0.002 a	32.63 ± 0.310 c	3.82 ± 0.036 c
M. persicae	280.20 ± 3.82 c	$0.152 \pm 0.001 \ b$	1.165 ± 0.002 b	$36.99 \pm 0.458 \text{ b}$	$4.55 \pm 0.054 \ b$
B. brassicae	266.66 ± 6.30 c	0.147 ± 0.002 c	1.158 ± 0.002 bc	$37.98 \pm 0.362 \text{ ab}$	$4.71 \pm 0.048 \ b$
L. erysimi	$200.88 \pm 4.63 \text{ d}$	0.135 ± 0.003 c	1.145 ± 0.003 c	39.26 ± 0.561 a	5.13 ± 0.074 a
*F-value	69.43	42.38	41.00	30.58	61.75

Data is Mean \pm S.D.

*P < 0.0001; d.f. = 5,54; Tukey's range = 4.178

Different letters mean significance within the distribution

Discussion

All six aphid species were essential foods for *H. variegata*. *Aphis gossypii* supported the highest fecundity, percent oviposition and oviposition period of *H. variegata*, which indicates its palatability, high nutritive contents and energetic values (Pervez and Omkar 2004a; Omkar and Mishra G. 2005; Keshavarz et al. 2015). The fecundity recorded in the current study on *A. gossypii* (1210.8 ± 55.31 eggs with upper range at 1469 eggs) is greater than those in earlier reports (841.5 eggs *M. persicae* by Lanzoni et al. 2004; 959.6 eggs on *Dysaphis crataegi* (Kalt.) by Kontodimas and Stathas 2005; 587.31 eggs on *Sitobion avenae* Fab. by Moghaddam et al. 2016; 667.12 ± 73.55 eggs on *A. gossypii* by Wu et al. 2010). This record fecundity is largely ascribed to its host-plant, *L. vulgaris*, as other factors were similar in the previous comparative studies. Nutritional aphids are consumed more

(Pervez and Omkar 2005), which supports increased oviposition leading to a high conversion efficiency of food biomass to progeny (Omkar and Pervez A. 2004). Significantly strong positive correlation between fecundity and egg viability indicates a diet dependent quantitative egg production that may also lead to the quantitative fertility and progeny sustenance. Similarly, a strong positive correlation between fecundity and the oviposition period indicates that high egg-production also extends the ladybird's reproductive phase. This enhanced reproductive-phase perhaps trade-offs with non-reproductive phase, i.e. resulting in much-reduced pre- and postoviposition periods.

Age-specific fecundity of *H. variegata* followed a triangular pattern (Dixon and Agarwala 2002) with positively skewed high peaks of oviposition when fed on aphids, *A. gossypii, A. craccivora* and *U. compositae*. This shows the best reproductive rate during the early phases of reproductive age. Better

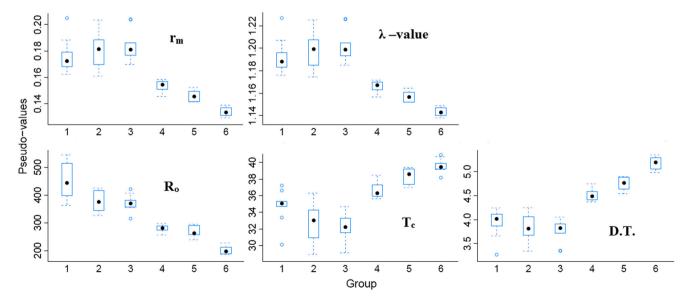


Fig. 2 The Box and Whisker plots of the pseudo-values of demographic parameters of *H. variegata* using six aphid-diets (1 = A. gossypii, 2 = A. craccivora, 3 = U. compositae, 4 = M. persicae, 5 = B, brassicae &

6 = L. erysimi), (r_m = intrinsic rate of increase, λ = finite rate of increase, R_o = Net reproductive rate in number of eggs/female/female. T_c = Mean generation time in days, D.T. = Doubling Time in days)

nutrient and energy contents of these aphids might be the reason for this high quality and rapid reproduction. Similar fecundity patterns using *A. gossypii* and *A. craccivora* as prey have also been reported in *P. dissecta* (Pervez and Omkar 2004a, 2004b; Omkar and Mishra G. 2005) and *Anegleis cardoni* (Weise) (Omkar et al. 2009). The peak was negatively skewed when fed on *B. brassicae* and *L. erysimi*, which shows that the peak was greatly delayed and attained in the later phase of reproductive age. Toxic biochemical contents in these aphids might have hampered the ovariole maturation leading to the negatively skewed fecundity function of the ladybird (Branquart and Hemptinne 2000).

Demographic analysis reveals that H. variegata performed well on A. craccivora with higher values of intrinsic and finite rates of increase supported by the shortest mean generation and doubling times. This agrees with previous similar studies on this aphid species using Oriental ladybirds, viz. Anegleis cardoni (Weise) (Omkar et al. 2009), Propylea dissecta (Mulsant) (Pervez and Omkar 2004b; Omkar and Mishra G. 2005) and Menochilus sexmaculatus (Fabricius) (Patel 2015; Privadarshani et al. 2016). Contrarily, A. craccivora reared on Vicia faba L. delayed the development of immature stages leading to eclosion of lighter-weight adults with heavy mortality in the European ladybird, Propylea quatuordecimpunctata (L.), (Kalushkov and Hodek 2005). Since aphid sequesters allelochemicals, e.g. linamarin from certain host plants, it is therefore restrained from utilizing plant proteins and thereby becomes less nutritious and unpalatable to the predators (Pratt 2008; Riddick et al. 2011). We, therefore, infer A. craccivora to be nutritious to H. variegata as it is to other indigenous ladybirds if fed on D. lablab (as in the present and other studies).

We found highest R_0 -value (449.45 ± 20.53 females/ female) on A. gossypii, which was much higher than those recorded when H. variegata was fed on the same but different five host-plants ranging from 153.98 to 199.03 females/ female (Wu et al. 2010). Similarly, the Ro-values of this predator feeding on D. noxia reared on two wheat cultivar-varieties, viz. Omid (399.35 ± 53.01) and Sardari (221.56 ± 34.68) was lesser than our data (Zanganeh et al. 2015). The same predator feeding on aphid, S. avenae reared on four hosts resulted in R_o-values ranging from 134.30 to 291.14 females/ female (Moghaddam et al. 2016). Comparing our results from these recent similar studies we may recommend A. gossypii reared on L. vulgaris for the augmentative rearing of the ladybird understudy. Furthermore, the data in these studies could not be compared within various group-levels due to the usage of parallel statistical approaches that lack jackknife technique.

Our results indicate that despite of suboptimal demographic parameters, *H. variegata* did not reject *B. brassicae* and this prey too falls in the category of essential prey. *Brassica* crops contain allelochemicals that shield their herbivores from predators (Ahuja et al. 2010). The lesser suitability of *B. brassicae* and *L. erysimi* to *H. variegata* could be ascribed to glucosinolates that aphids sequester from *Brassica* crops and get degraded due to endogenously produced thioglucosidase when predators seize aphids (Jones et al. 2002; Bridges et al. 2002; Husebye et al. 2005). Contrarily, the seven-spotted ladybird, *Coccinella septempunctata* Linnaeus considers *L. erysimi* reared on *B. campestris* as most palatable and nutritious food (Omkar and Srivastava S. 2003). The degraded and hydrolyzed glucosinolates can form isothiocyanates, thiocyanates, nitriles, and epithionitriles, which are toxic to predators. In addition, the white powdery layers on the body of *B. brassicae* probably make it less attractive to aphidophagous ladybirds.

In brief, we conclude that: (i) all six aphids tested are essential foods with prey suitability in the rank order: A. gossypii > A. craccivora > U. compositae > M. persicae > B. brassicae > L. erysimi, (ii) A. craccivora reared on D. lablab is highly suitable for the improved reproduction and demography of H. variegata, (iii) Brassica hosted aphids, B. brassicae and L. erysimi would not be recommended for augmentation of H. variegata, and (iv.) this prospects of augmentative rearing of this ladybird are very high when reared on A. gossypii, A. craccivora and U. compositae using suitable host-plants.

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Compliance with ethical standards

The authors declare that they have prepared the manuscript by the compliance with ethical standards. All the authors read and approved the final manuscript. The manuscript has been prepared by the consent of all the authors.

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

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