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ARTICLE

Optimising aphid biocontrol with the predator *Propylea dissecta*, based on experimental evolution of a predatory population

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Abstract

Intraspecific variation is the variation in morphology, physiology, behaviour, and social organisation of any species as it adapts to changing environmental circumstances by varying its feeding habits. In the present study, we investigated the disparities between the preselected (F1) and postselected (F15) populations of *Propylea dissecta* Mulsant (Coleoptera: Coccinellidae) when fed on four different prey species, namely *Aphis gossypii* Glover from bottle gourd, *Lagenaria vulgaris* Seringe (Cucurbitaceae), *Lipaphis erysimi* (Kaltenbach) from mustard, *Brassica campestris* Linnaeus (Brassicaceae), *Rhopalosiphum maidis* (Fitch) from maize, *Zea mays* Linnaeus (Poaceae), and *Uroleucon compositae* (Theobald) from chrysanthemum, *Chrysanthemum indicum* Linnaeus (Asteraceae), under an experimental evolution study. A simple bimodal pattern of distribution was obtained for each prey species, which was warped with variations in prey species for both F1 and F15. This research might provide the basis for further studies on the differential pace of development of various other prey species, improve understanding of ecological evolution, and provide a spectrum of fast-growing bioagents for the introduction of biological control strategy in pest management techniques against agropests.

Introduction

It is well known that the ladybird beetles (Coleoptera: Coccinellidae) prey upon and consume a broad range of prey, including aphids (Hemiptera: Aphidoidea) and other soft-bodied insects, mites (Acariformes), and fungi, as well as pollen, nectar, and other plant products (Hodek and Honek 1996; Dixon 2000). The efficacy of aphids as a source of nourishment for ladybird beetles' growth, development, survival, and reproduction varies (Pervez and Omkar 2004; Nyaanga *et al.* 2012). However, an aphid species suitable for one ladybird may not be suitable for other ladybirds. Some ladybirds appear to attack and consume many species of prey, whereas others have been recorded to selectively attack and consume few prey species. This may be due to differences in the chemical constituents of different aphid species and the differential nutritional requirements of ladybirds (Dixon 2000). Ladybirds demonstrate habitat specialisation, and whether they attack a few or many prey species may be related in part to the number of prey species they regularly encounter in their respective habitats (Hodek and Honek 1996) and the beetles' own nutritional requirements.

Many reports exist on the impact of different prey species on insect predators (Stamp and Meyerhoefer 2004; Ishiguri and Toyoshima 2006). Due to their economic and biological value,

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several ladybird beetle species have been studied for prey-dependent reactions, namely *Propylea quatuordecimpunctata* Linnaeus (Rogers *et al.* 1994), *Coelophora saucia* (Mulsant) (Pathak 2008), *Scymnus frontalis* Fabricius (Gibson *et al.* 1992), *Harmonia axyridis* Pallister (Kalaskar and Evans 2001), *Coccinella septempunctata* Linnaeus (Kalushkov and Hodek 2004), *P. dissecta* (Omkar and Mishra 2005), *Anegleis cardoni* (Weise) (Afroze 2000; Omkar *et al.* 2011), and many more, but experimental evolution studies on prey–predator interactions regarding this beetle and other insect predator species are few.

Previous research has shown that when *H. axyridis* larvae were grown on *Aphis spiraecola* (Hemiptera: Aphididae) (Patch), a considerable number of individuals lived to maturity (70%) but with low oviposition status (Michaud 2000). Other research that involved *Lipaphis pseudobrassicae* Linnaeus (Hemiptera: Aphididae) showed it was high-quality prey for *C. septempunctata* but not appropriate for the development of *Micraspis discolour* (Fabricius) (Coleoptera: Coccinellidae) (Agarwala *et al.* 1987). When *Menochilus sexmaculatus* (Fabricius) (Coleoptera: Coccinellidae) was provided with the aphids *Melanaphis sacchari* (Zehntner), *Hyadaphis coriandri* (Das), and *Brevicoryne brassicae* (Linnaeus), the maximum reproduction was found with *M. sacchari*, followed by *H. coriandri* and *B. brassicae* (Bind and Omkar 2004). Regardless of so many lucid experiments on prey species having been undertaken, many questions remain regarding the study of experimental evolution. In the present analysis, we determined the impact of prey suitability on the F1 and F15 generation developmental variants (*i.e.,* slow and fast developers) of *P. dissecta* and whether the selection has a major effect on the developmental and reproductive attributes of the two variants when fed on four different prey species.

Materials and methods

Stock maintenance

Adults of *P. dissecta* were gathered from aphid-infested agricultural fields and gardens surrounding Lucknow, Uttar Pradesh, India (26° 50′ N, 80° 54′ E) and brought to the laboratory for initial stock maintenance. They were reared in plastic Petri dishes (9.0 × 2.0 cm) with pea aphid, *Acyrthosiphon pisum* (Harris) (Hemiptera: Aphididae), and maintained on broad bean, *Vicia faba* Linnaeus (Fabaceae), taken from maintained glasshouse cultivation. Following Siddiqui *et al.* (2015), the Petri dishes were kept under standard laboratory conditions in biological oxygen demand incubators. Ten-day-old, sexually mature male and female *P. dissecta* were paired in the aforementioned Petri dishes. The first five days of oviposition were observed. Following that, eggs were separated into individual Petri dishes. After hatching, larvae were provided aphid prey, as described before, supplemented every 24 hours. Individual *P. dissecta* that had just emerged were maintained individually under the aforementioned laboratory conditions, and the necessary stages were used for the study.

Selection for developmental rate lines

A total of 200 individual *P. dissecta* (*i.e.,* 100 males and 100 females) were collected from the captive stock described above. For line separation, we reared beetles on the aforementioned aphid prey for normalisation to avoid errors. To maintain the stock, the rearing method was followed as described before for 15 generations. Following Mishra and Omkar (2012), all newly emerged individuals of each generation were separated and categorised as either "slow developers" or "fast developers" and were reared individually until maturation. Neonates with a short total developmental stage were categorised as "fast developers" (test-driven development, in days ± standard error: 10.21 ± 0.01), whereas those with a prolonged developmental stage were categorised as "slow developers" (test-driven development, in days ± standard error: 12.10 ± 0.01). Further separation processes were performed by following Siddiqui *et al.* (2015).

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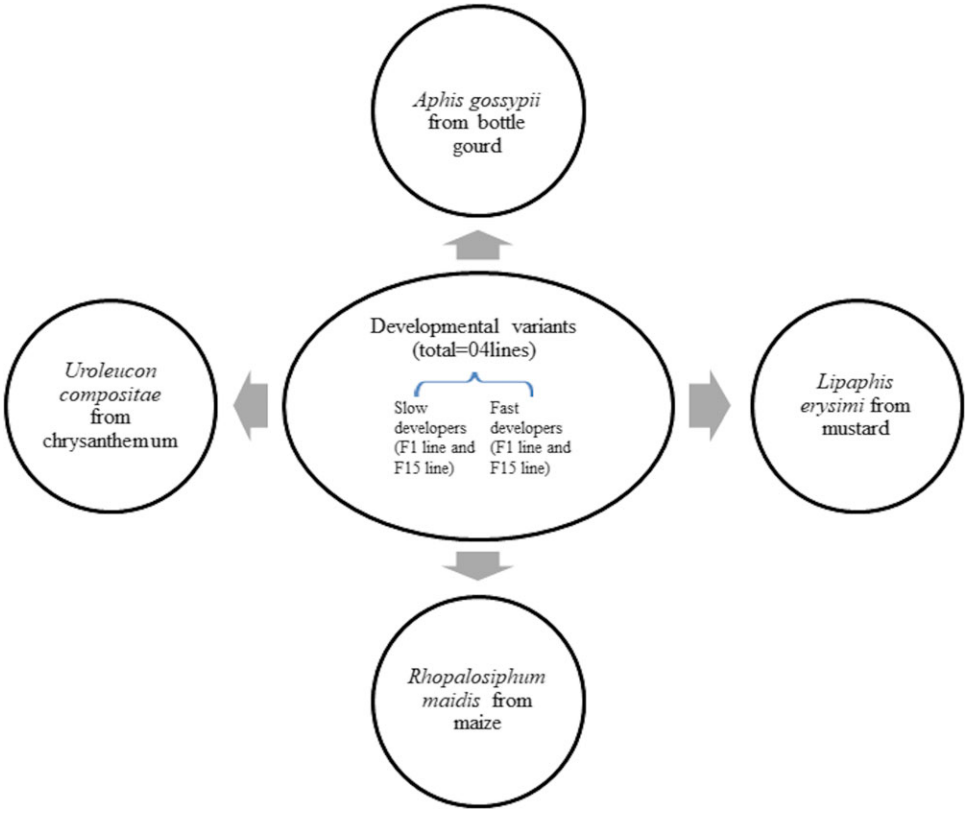

Fig. 1. Aphid–host complexes chosen for experimental design for *Propylea dissecta* on four different aphid prey for both slow and fast developers of both F1 and F15 generations, respectively.

Experimental design

Aphis gossypii Glover from bottle gourd, *Lagenaria vulgaris* Seringe (Cucurbitaceae), *Lipaphis erysimi* (Kaltenbach) from mustard, *Brassica campestri* Linnaeus (Brassicaceae), *Rhopalosiphum maidis* (Fitch) from maize, *Zea mays* Linnaeus (Poaceae), and *Uroleucon compositae* (Theobald) from chrysanthemum, *Chrysanthemum indicum* Linnaeus (Asteraceae) were the aphid–host plant complexes that were chosen for the experimental design illustrated in Figure 1.

Ten-day-old unmated *P. dissecta* adults that had been identified and isolated as slow and fast developers were paired with their developmental type. Each separated line and the control were able to mate in their separate plastic Petri dishes (9.0 × 2.0 cm), where they were fed with any of the four prey species, namely *A. gossypii*, *L. erysimi*, *R. maidis*, and *U. compositae*. The first five days of oviposition (= 300 eggs from each line) of each line on the above prey species were examined. Until adult emergence, *P. dissecta* hatchlings were raised separately in Petri dishes (size as before) on the same prey species as their parents had been. The larvae were monitored twice a day for survival and moulting. The second and third instars of each prey were given to each *P. dissecta* line's hatched larvae. Using an electronic balance (Sartorius CP225-D; 0.01 mg precision; Sartorius, Goettingen, Germany), aphids were weighed (aphid prey weighed approximately 30 mg for the first- and second-instar beetles, and approximately 50 mg for the third- and fourth-instar beetles and for the adults). Based on their total developmental duration, the beetle instars were classified as slow or fast developers for both the control and selected lines, according to Mishra and Omkar (2012). Emerging adult beetle body mass was measured after 6 hours of emergence.

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Table 1. Normality of duration of developmental variants in control (F1) and selected line (F15) of *Propylea dissecta* on different prey species.

Prey species	Developmental variants	Generations	Normality of data
Aphis gossypii	Slow developers	Control (F1)	D+: 0.048 D–: 0.058 D: 0.058; $P > 0.15$
		Selected line (F15)	D+: 0.030 D–: 0.035 D: 0.035; $P > 0.15$
	Fast developers	Control (F1)	D+: 0.026 D–: 0.034 D: 0.034; $P > 0.15$
		Selected line (F15)	D+: 0.041 D–: 0.037 D: 0.041; $P > 0.15$
Rhopalosiphum maidis	Slow developers	Control (F1)	D+: 0.080 D–: 0.087 D: 0.087; $P > 0.15$
		Selected line (F15)	D+: 0.102 D–: 0.085 D: 0.102; $P > 0.15$
	Fast developers	Control (F1)	D+: 0.064 D–: 0.052 D: 0.064; $P > 0.15$
		Selected line (F15)	D+: 0.030 D–: 0.045 D: 0.045; $P > 0.15$
Lipaphis erysimi	Slow developers	Control (F1)	D+: 0.065 D–: 0.065 D: 0.065; $P > 0.15$
		Selected line (F15)	D+: 0.058 D–: 0.053 D: 0.058; $P > 0.15$
	Fast developers	Control (F1)	D+: 0.098 D–: 0.100 D: 0.100; $P > 0.15$
		Selected line (F15)	D+: 0.070 D–: 0.073 D: 0.073; $P > 0.15$
Uroleucon compositae	Slow developers	Control (F1)	D+: 0.047: D–: 0.074 D: 0.074; $P > 0.15$
		Selected line (F15)	D+: 0.065 D–: 0.067 D: 0.067; $P > 0.15$
	Fast developers	Control (F1)	D+: 0.048 D–: 0.049 D: 0.049; $P > 0.15$
		Selected line (F15)	D+: 0.072 D–: 0.063 D: 0.072; $P > 0.15$

Statistical analysis

To test bimodal distribution, data on the total developmental duration for both control and selected *P. dissecta* lines fed on each prey species were tested by the Kolmogorov–Smirnov normality test (Table 1), and frequency data on the same were found to be bimodal (Fig. 2). For the comparison of (1) slow and quick emergence ratios and (2) overall survival, a Chi-square "goodness of fit" analysis was performed. The data were calculated using a general linear multivariate analysis of variance with generation (control and selected line), prey species, and developmental variation (slow *versus* fast) as independent variables and total developmental duration and adult body mass as dependent variables.

Before the analysis of variance, percent data were arcsine-transformed, and Tukey's *post hoc* comparison of means was used before subjecting the fecundity and percent egg viability data to a three-way analysis of variance. The data on generation (F1 and F15 generations), prey species, and developmental variation (slow *versus* fast) were assessed for normal distribution. *Post hoc* Tukey's test of honestly significant difference at 5% levels was used to determine differences between activity means. We used Minitab 15.0 software (https://www.minitab.com/en-us/products/minitab) for all statistical analyses.

Results

The fecundity of postselected (F15) fast-developing *P. dissecta* females was higher than that of preselected (F1, or control) fast-developing females, but the opposite was found for slow-developing *P. dissecta* reared on *A. gossypii*. Both the selected slow developers and selected fast developers showed enhanced fecundity on *L. erysimi* and *U. compositae* diet (Fig. 3A). Results of two-way analysis of variance revealed that the impacts of prey species and generation on the fecundity of both developmental variations of *P. dissecta* were statistically

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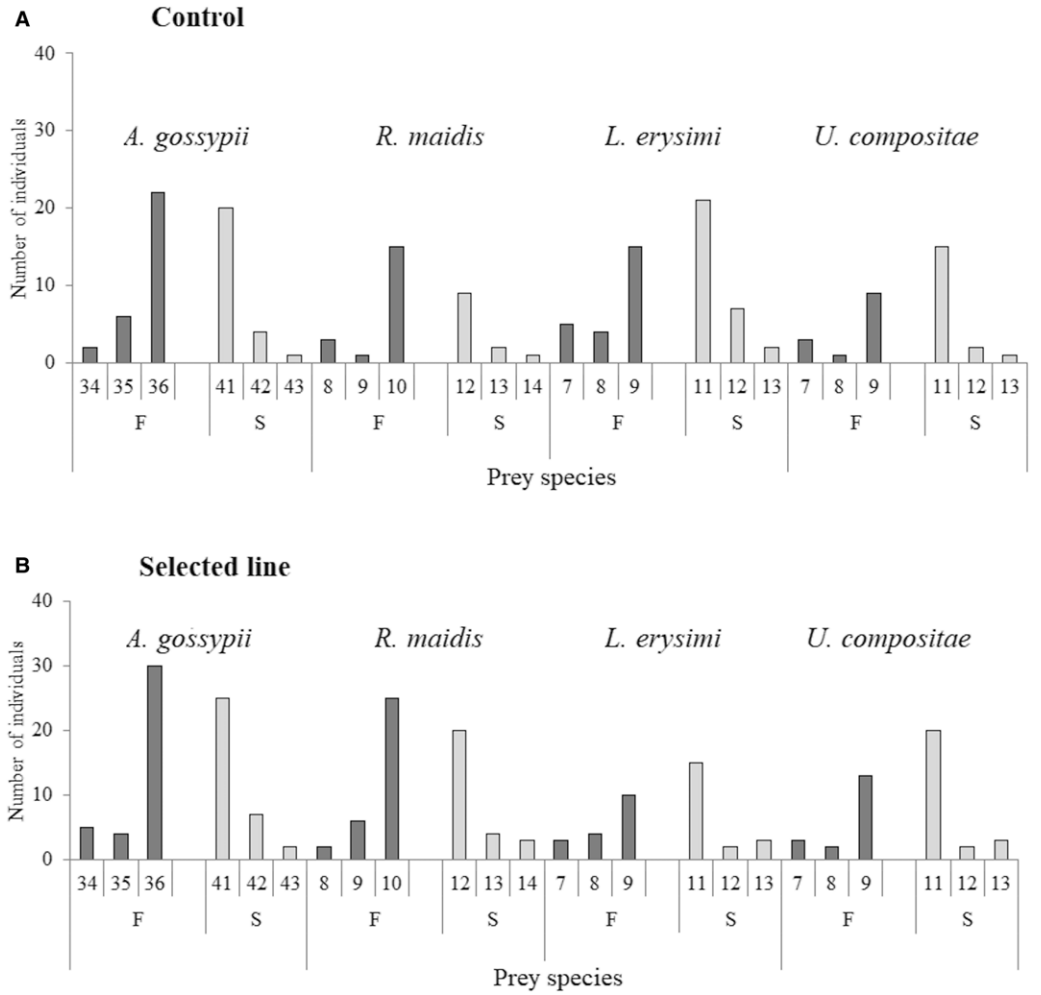

Fig. 2. Frequency distribution of total developmental duration (TDD; in days) of **A**, F1 and **B**, F15 generation of slow and fast developers on four different prey species. Bars indicated number of individuals emerging at each development duration. "*F*" indicates fast developers, and "S" indicates slow developers of each prey species. Prey species are *Aphis gossypii* from *Lagenaria vulgaris*, *Lipaphis erysimi* from *Brassica campestri*, *Rhopalosiphum maidis* from *Zea mays*, and *Uroleucon compositae* from *Chrysanthemum indicum*.

significant, but the interaction between prey species and generation (preselected and postselected) on the reproductive attribute was statistically negligible.

The percent egg viability of selected fast-developing *P. dissecta* females was higher than that of preselected fast-developing females, but the opposite was found for slow-developing *P. dissecta* reared on *A. gossypii*. Selected slow-developing *P. dissecta* showed enhanced fecundity on *L. erysimi* and *U. compositae* (Fig. 3B).

The emergence ratio of pre- and postselected slow- and fast-developing *P. dissecta* reared on different prey species differed significantly (Fig. 4). When the beetle larvae were fed *U. compositae*, the proportion of selected slow-developing specimens was highest; when larvae were fed *A. gossypii*, the slow-developing proportion was lowest. The maximum proportion of selected fast-developing *P. dissecta* was observed when larvae were fed *A. gossypii*, and the minimum was observed in the control group of fast-developing *P. dissecta* that were reared on *U. compositae* (Fig. 4).

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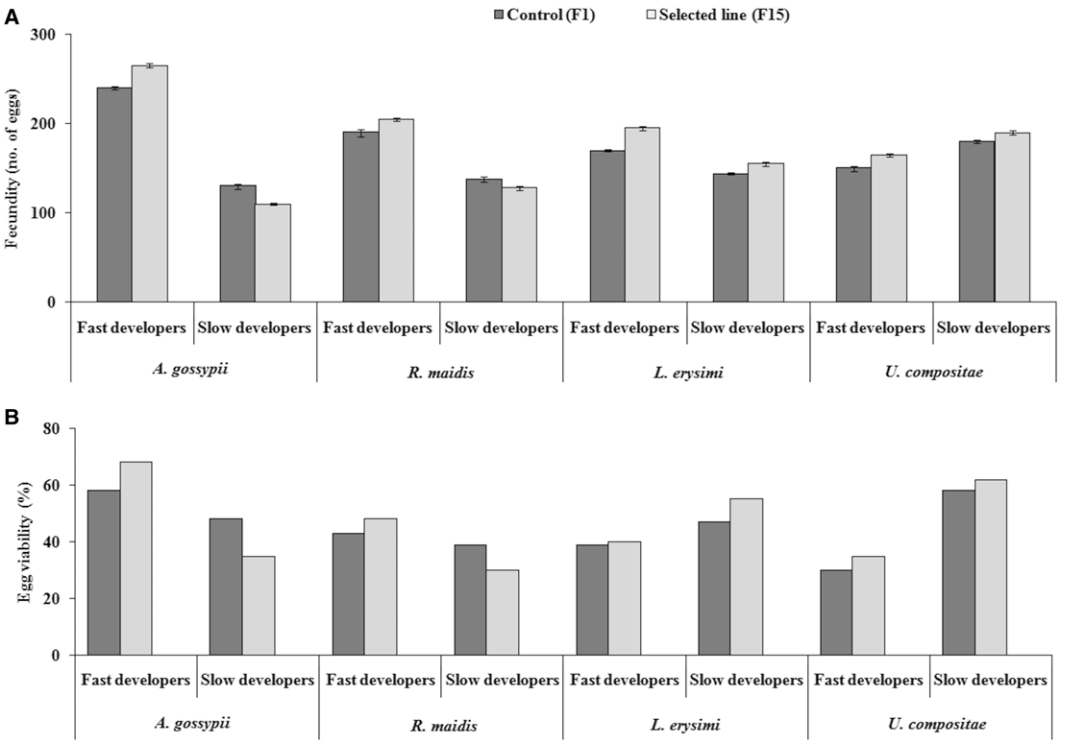

Fig. 3. A, Fecundity and **B**, percentage egg viability of control (F1) and selected lines (F15) of developmental variants of *Propylea dissecta* on different prey species, *Aphis gossypii, Lipaphis erysimi, Rhopalosiphum maidis*, and *Uroleucon compositae*.

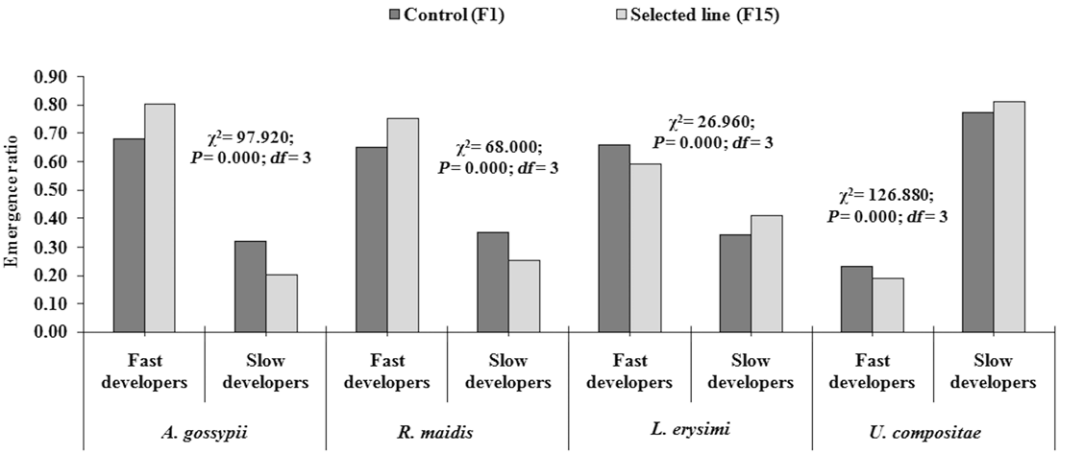

Fig. 4. Effect of prey species *Aphis gossypii*, *Lipaphis erysimi*, *Rhopalosiphum maidis*, and *Uroleucon compositae* on emergence ratio of developmental variants of control (F1) and selected line (F15) of *Propylea dissecta*. Chi-square (χ^2) value reveals comparison between developmental variants of both control and selected line.

Prey species, generation, and developmental variations had statistically significant influences on the total duration of the development of slow and fast developers. The interactions were also significant (Table 2). Postselected fast developers developed more quickly than preselected fast

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Table 2. Total development duration and body mass of control and selected line of slow and fast developers of *Propylea dissecta* on different prey species. Multivariate analysis of variance shows effect of prey species, generation, and developmental variants and their interactions on these parameters.

Prey species	Developmental variants	Generations	Total development duration (in days)	Body mass of adults (mg)
Aphis gossypii	Slow developers	Control (F1)	15.09 ± 0.10aB	11.92 ± 0.23bA
		Selected line (F15)	18.30 ± 0.14bB	10.47 ± 0.28aA
	Fast developers	Control (F1)	13.26 ± 0.12bA	15.17 ± 0.20aB
		Selected line (F15)	10.40 ± 0.13aA	18.83 ± 0.33bB
Rhopalosiphum maidis	Slow developers	Control (F1)	16.54 ± 0.19aB	11.90 ± 0.83bA
		Selected line (F15)	18.74 ± 0.33bB	08.09 ± 0.21aA
	Fast developers	Control (F1)	13.82 ± 0.21bA	12.93 ± 0.20aB
		Selected line (F15)	12.58 ± 0.16aA	15.19 ± 0.16bB
Lipaphis erysimi	Slow developers	Control (F1)	20.00 ± 0.12aB	09.93 ± 0.21bA
		Selected line (F15)	21.06 ± 0.19bB	08.23 ± 0.13aA
	Fast developers	Control (F1)	16.56 ± 0.07bA	11.94 ± 0.13aB
		Selected line (F15)	15.12 ± 0.12aA	13.37 ± 0.13bB
Uroleucon compositae	Slow developers	Control (F1)	23.40 ± 0.10aB	08.29 ± 0.13bA
		Selected line (F15)	23.10 ± 0.16aB	06.09 ± 0.10aA
	Fast developers	Control (F1)	20.04 ± 0.12bA	09.06 ± 0.12aB
		Selected line (F15)	18.50 ± 0.15aA	10.43 ± 0.20bB
$F_{\text{Prey species}}$, *P*-value, *df*			$F = 1286.44$, $P = 0.001$, $df = 3799$	$F = 336.62$, $P = 0.001$, $df = 3799$
$F_{\text{Generations}}$, *P*-value, *df*			$F = 3.93$, $P = 0.048$, $df = 1799$	$F = 1.93$, $P = 0.166$, $df = 1799$
$F_{\text{Developmental variants}}$, *P*-value, *df*			$F = 2174.22$, $P = 0.001$, $df = 1799$	$F = 722.82$, $P = 0.001$, $df = 1799$
$F_{\text{Prey species} \times \text{Generations}}$, *P*-value, *df*			$F = 12.43$, $P = 0.001$, $df = 3799$	$F = 8.73$, $P = 0.001$, $df = 3799$
$F_{\text{Prey species} \times \text{Developmental variants}}$, *P*-value, *df*			$F = 16.50$, $P = 0.001$, $df = 3799$	$F = 39.23$, $P = 0.001$, $df = 3799$
$F_{\text{Developmental variants} \times \text{Generations}}$, *P*-value, *df*			$F = 578.25$, $P = 0.001$, $df = 1799$	$F = 317.24$, $P = 0.001$, $df = 1799$
$F_{\text{Generations} \times \text{Developmental variants} \times \text{Prey species}}$, *P*-value, *df*			$F = 15.81$, $P = 0.001$, $df = 3799$	$F = 5.31$, $P = 0.001$, $df = 3799$

Values are mean ± standard error.
Lower-case letters represent comparison of means between slow–slow and fast–fast developers of both generations on each prey species.
Upper-case letters represent comparison of means between slow and fast developers of control and selected line within a prey species.

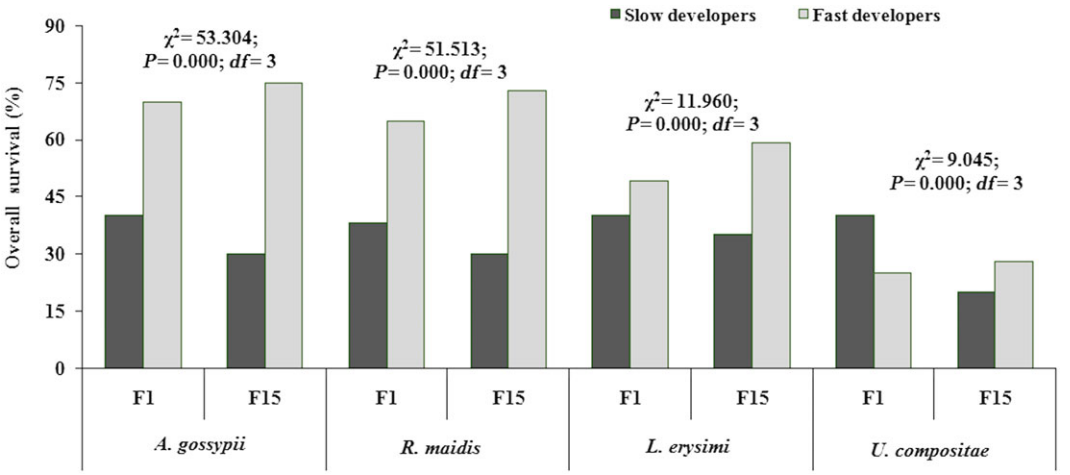

Fig. 5. Effect of prey species *Aphis gossypii*, *Lipaphis erysimi*, *Rhopalosiphum maidis*, and *Uroleucon compositae* on overall survival of control (F1) and selected line (F15) of developmental variants of *Propylea dissecta.*

developers did and gained maximum adult body mass regardless of which prey species they were reared on. Preselected slow developers developed more quickly than selected slow developers, gaining elevated adult body mass regardless of the prey species. In both pre- and postselected fast developers, the shortest total developmental period occurred when the larvae were fed *A. gossypii*, and the longest total developmental period occurred when the larvae were fed *U. compositae*. The opposite was observed in slow developers, which developed quickest on *U. compositae* and slowest on *A. gossypii.*

The overall survival percentages of the control and selected lines of slow and fast developers were found to differ substantially. The greatest survival occurred in selected fast developers fed on *A. gossypii* and the least survival occurred in selected slow developers fed on *U. compositae* (Fig. 5).

Discussion

Plasticity was found in the development of immature stages of *P. dissecta* from egg to adult for up to 15 generations. The coexistence of two developmental rate variants within an egg batch has been observed in a variety of taxa, including ladybirds (Singh and Mishra 2016) and other insects (Gouws *et al.* 2011), and after intrinsic selection of slow and fast developers, Siddiqui *et al.* (2015) observed a well-marked difference in predatory response of *P. dissecta*.

It is clear from the results of the present study that prey consumption by different life stages of ladybirds varied with aphid prey. In *Propylea dissecta*, the selected line of fast developers showed a well-marked feeding preference for various aphid species, with highest consumption of *A. gossypii* and lowest consumption of *U. compositae*. This might be due to conditional rearing, wherein the larvae must survive on available resources. The rate of consumption by selected lines of fast-developing *P. dissecta* may also be affected by the aphid prey species and their various biological constituents (Dixon 2000). According to Colburn and Asquith (1970) and Obata (1986), aphid-produced chemicals (kairomones) may also make predators more voracious at different stages of their life cycles, likewise permitting fast-developing individual to become more capable of responding to *A. gossypii* than to *U. compositae*. Aphid size may be another factor: as prey size increases, the capture rate by predators declines because larger prey are better able to escape (Chau and Mackauer 1997); that is, small aphid prey are more

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easily caught by fast-developing *P. dissecta*, and because catching larger prey requires more time and effort, fast-developing predators typically avoid larger prey. Slow developers, on the other hand, appear to have a contradictory response: Siddiqui *et al.* (2015) observed that slow-developing predators had the greatest attack rate and the longest handling time, suggesting that these predators enhance their energy returns by feeding on large prey (Schoener 1969).

In the present study, both control and selected fast-developing *P. dissecta* reared on *U. compositae* had poor growth and reproductive performance, perhaps because of chemicals produced by the aphids' host plant (Seiber *et al.* 1982; Morsy *et al.* 2001). However, control and selected slow-developing *P. dissecta* reared on *U. compositae* were not affected. The differences in growth and performance that were observed may be due to differences in prey compatibility, which is based on the physiological state of the host plant, aphid efficiency, and nutritional budgets (Soares *et al.* 2004).

The nutritional composition of aphid populations might explain the significant variation in predator reproduction. Aziz *et al.* (1970) reported a species-specific feeding preference in *C. septempunctata*, which laid more eggs when fed on *L. erysimi* than on *A. gossypii*. However, in the present study, higher fecundity was found in postselected fast developers than in pre- and postselected slow developers; this can probably be attributed to the early maturation of an increased number of ovarioles, which is also likely to be dependent on the prey consumption and nutritional quality of *A. gossypii.* In previous research, selected fast developers were also observed to have higher consumption than pre- and postselected slow developers on *A. pisum* (Siddiqui *et al.* 2015), and the consumption study should be extended to support this concept on other aphid prey species as well.

Bueno and Lopez-Urrutia (2012) provided another study model, which indicated that an organism with a shorter developmental time produces more offspring. The findings, however, highlighted a trade-off between reproduction and survival (Scannapieco *et al.* 2009; Lazarevic *et al.* 2012). Slow developers invest most of their resources in physiological maintenance (Kuzawa 2008).

With changes in prey organisms, the ratio of pre- (control = F1 generation) to postselected (selected = F15 generation) slow- and fast-developing ladybird beetles changed. As observed in the present study, the optimal prey promotes faster development, results in lower mortality of larvae (Chen *et al.* 2012), and yields larger adults (Michaud 2005). As a result, selected fast-developing *P. dissecta* fed on *A. gossypii* and *L. erysimi* probably were able to develop more effectively and in greater numbers than the F1 (control) generation was able to. More slow-developing *P. dissecta* were found on *U. compositae,* which are known to be suboptimal prey, having low nutrition (Omkar and Bind 2004). Such a stressful diet may be unsuitable for fast-developing predators, and their increased mortality on *U. compositae* may have skewed the ratio in favour of slow developers under less favourable conditions, as was found in the present study. The varying ratios of slow *versus* fast developers according to prey species may indicate increases in the mortality of particular developmental predator variants (slow *versus* fast developers) unable to meet the required threshold mass for the next developmental stage when fed on each prey species. As a result, we found that the overall fitness promoted by prey species, or the overall suitability of prey species for selected fast developers, was ranked as follows:

$$A.\,gossypii > R.\,maidis > L.\,erysimi > U.\,compositae$$

The present study shows that each aphid species had a considerable impact on the life qualities of the developmental variants of both generations (F1 and F15) of *P. dissecta,* with some prey species being more suitable than others. The existence of both developmental variants on all prey species in both the F1 and F15 generations changed with the prey species. We observed elevated performance in selected (F15) fast developers compared to that in preselected (F1)

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fast developers, and we recorded the most selected fast developers on *A. gossypii,* which was probably the most nutritious prey, and fewest on *U. compositae*, which was the least nutritious prey. Fast developers were observed to be heavier than slow developers, and the selected fast developers fed on *A. gossypii* produced more eggs with greater egg viability. Preselected (F1) slow developers gained the most body mass within a depressed developmental time than selected slow developers did. In this way, the study indicates increased survival of predators on better-suited prey species that was achieved through a process of selection that generally resulted in increased fitness after generational rearing, in comparison to lower survival of predators on less-suited food conditions or in a preselected generation of predator (= F1 generation or control individuals).

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