

Slow and fast development in two aphidophagous ladybirds on scarce and abundant prey supply

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Abstract

Developmental rates are highly variable, both within and between genotypes and populations. But the rationale for two differential (slow and fast) developmental rates within same cohort under varying prey supply has yet not been explored. For this purpose, we investigated the effect of scarce and abundant prey supply on slow and fast development at 27°C in two aphidophagous ladybirds, *Menochilus sexmaculatus* (Fabricius) and *Propylea dissecta* (Mulsant) and its effect on their body mass and reproductive attributes. The ladybirds were provided with scarce and abundant supply of *Aphis craccivora* Koch under standardized abiotic conditions in the laboratory. A clear bimodal (two peaks, where the first peak represented the fast developing individuals and the second peak slow developing individuals) pattern of distribution for both prey supplies was obtained, which got skewed with change in prey supply. On abundant prey supply, more fast developing individuals (139 *M. sexmaculatus* and 123 *P. dissecta*) were found and less (46 *M. sexmaculatus* and 36 *P. dissecta*) on scarce prey supply. Slow developing individuals had female biased sex ratio, higher longevity and lower body mass. Fast developing females laid higher number of eggs with higher egg viability. Results of the study are indicative of occurrence and constancy of the slow and fast developing individuals in the egg batch.

Keywords: coccinellidae, developmental duration, *Menochilus sexmaculatus*, prey quantity, *Propylea dissecta*, slow:fast emergence

(Accepted 17 December 2015; First published online 22 February 2016)

Introduction

The development of individuals plays an important role in regulating the population of an organism in an agroecosystem. Development varies interspecifically and intraspecifically in response to various abiotic and biotic factors. Interspecific variation includes the slow–fast continuum which elucidates the occurrence of wide variations in sizes of organisms owing to variation in developmental rates (Oli, 2004; Bielby *et al.*, 2007). According to this, fast life history is characterized by early reproduction, high fecundity, short generation time, short life-span, small offspring and adult body size; while a slow life history has the opposite characteristics (Sibly & Brown, 2007;

Jeschke & Kokko, 2009). Intraspecific variation on the other hand, includes the occurrence of individual differences within a population in response to various genetic and environmental factors. Individual development typically exhibits plasticity in response to the prevailing environmental conditions (Pigliucci, 2001), especially temperature. Shifts in temperature even minor ones are known to cause changes in developmental and survival responses of most organisms (Joschinski *et al.*, 2015). This developmental plasticity often involves a strong genetic component (Bergland *et al.*, 2008; Beldade *et al.*, 2011), individual condition and state (Hiyama *et al.*, 2012), transgenerational effects (Greer *et al.*, 2011) and multifactorial inheritance (Bergland *et al.*, 2008; Maleszka, 2008). The relationship between development and physiology helps in the translation of genotypes into phenotypes and thus is likely to have major effects on evolutionary outcomes (Stern, 2010).

However, what is not understood is the presence of different rates of development in a single cohort under similar abiotic and biotic conditions. Studies on several taxa have

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revealed the occurrence of two distinct rates of development within a cohort (e.g., Gross, 1985; Schönrogge *et al.*, 2000; Witek *et al.*, 2006; Skorping, 2007; Lewis *et al.*, 2010). This was investigated and formally reported in the ladybirds, *Menochilus sexmaculatus* (Fabricius) and *Propylea dissecta* (Mulsant) (Mishra & Omkar, 2012) and chrysomelid, *Zygogramma bicolorata* Pallister (Pandey *et al.*, 2013) under constant conditions as well as in the two ladybirds in response to variations in temperature (Singh *et al.*, 2014, 2016). Temperature in particular is one of the main driving forces of development (Jalali *et al.*, 2014; Benelli *et al.*, 2015) and feeding rates (Sentis *et al.*, 2012; Sørensen *et al.*, 2013) in coccinellids.

Genetic variations in phenotypic plasticity for developmental rates and size in sub-populations have been used to select for faster developing organisms in *Drosophila melanogaster* Meigen (Partridge & Fowler, 1992), lepidopteran, *Manduca sexta* (L.) (D'Amico *et al.*, 2001) and the ladybird, *Hippodamia convergens* (Guérin-Méneville) (Rodríguez-Saona & Miller, 1995), but under constant abiotic and biotic conditions. Bimodal (two peaks i.e., slow and fast) distribution has been reported not only in intraspecific body size (Gouws *et al.*, 2011) but also in the developmental rates (Mishra & Omkar, 2012; Singh *et al.*, 2014, 2016). The bimodal distribution and the proportion of slow:fast emergence has been found to shift in *M. sexmaculatus* and *P. dissecta*, with change in abiotic conditions like temperature and photoperiod (Singh *et al.*, 2014, 2016). The ratio of slow and fast developing individuals also differs with the biotic conditions, such as prey; poor prey species favoured the emergence of more slow developing individuals and vice versa (Singh *et al.*, unpublished data). Such trends in slow:fast ratio have been attributed to selective mortality influenced by the prevailing abiotic and biotic conditions.

Every organism requires a certain amount of energy for growth, development and survival. Favourable conditions with adequate food and energy resources combined with a congenial environment maximize the survival of organisms. Since aphid availability in the agroecosystem frequently fluctuates in space and time, the ladybird predators often face the problem of prey scarcity/deprivation. Prey deprivation severely affects the life attributes of ladybirds (Omkar & Pervez, 2003; Schuder *et al.*, 2004; Phoofole *et al.*, 2008; Santos-Cividanes *et al.*, 2011). Both larval and adult performances of different predatory ladybirds are constrained by the quantity of prey (Lee & Kang, 2004; Santos-Cividanes *et al.*, 2011). While evaluating the developmental time and survival of *Scymnus subvillosus* (Goeze) at different prey densities, Atlihan & Guldal (2009) found that increased prey density reduced the developmental time and mortality rate. The developmental durations of larval instars of *Coccinella septempunctata* L. and *Coccinella transversalis* Fabricius were short when prey was present in abundance and the larvae pupated earlier (Maurice & Kumar, 2011). Prey quantity severely affects the reproductive output and fitness of ladybirds (Agarwala *et al.*, 2001; Omkar *et al.*, 2010). Clutch size and oviposition rate is known to be influenced by the prey quantity available to females at the time of oviposition (Dixon, 2000). Ware *et al.* (2008) found the clutch sizes to be maximum when females of *Harmonia axyridis* (Pallas) and *Adalia bipunctata* L. were reared on abundant prey. Agarwala *et al.* (2009) reported that females of *Harmonia dimidiata* (Fabricius) mature earlier and produce more eggs at high prey density. In general, quantity of prey is the key component that affects

development, survival and reproduction of insect predators, including ladybirds (Omkar *et al.*, 2010; Dmitriev & Rowe, 2011). Therefore, it is logical to hypothesize that the proportion of slow and fast developing individuals will possibly change with change in prey quantity.

Owing to the prominent impact of prey quantity on the development in ladybirds, in the present study we decided to investigate: (i) the effect of scarce and abundant prey supply on the phenomena of slow and fast development in two locally abundant aphidophagous ladybirds, *M. sexmaculatus* and *P. dissecta*; (ii) the proportion of slow and fast developing individuals in a cohort with varying prey supply and (iii) the variation in developmental and reproductive attributes of these developmental types. Both these ladybirds co-exist as predators of the numerous species of aphids that infest agricultural crops grown around Lucknow, India. Both ladybirds are polyphagous and potential biocontrol agents. The results of this study are expected to improve our understanding of the specific mechanism involving the slow and fast development in relation to scarce and abundant prey supply.

Materials and methods

Two predaceous ladybirds, *M. sexmaculatus* and *P. dissecta*, were selected for the study owing to their: (a) local abundance, (b) wide prey range, (c) fast development, (d) high reproduction and (e) previous studies on related aspects (Mishra & Omkar, 2012; Singh *et al.*, 2014, 2016).

Stock maintenance

Adults of *M. sexmaculatus* and *P. dissecta* were collected from agricultural fields surrounding Lucknow, India (26°50' N, 80°54' E) and brought to the laboratory. They were paired and kept in transparent plastic Petri dishes (9.0 × 2.0 cm²) containing daily replenished aphids, *Aphis craccivora* Koch (on host plant *Vigna unguiculata* (L.) taken from polyhouse cultures; 25 ± 2°C; 65 ± 5% relative humidity (RH)) under standard laboratory conditions (27 ± 1°C; 65 ± 5% RH; 14L:10D) in incubators. Eggs laid were collected every 24 h and incubated under above abiotic conditions until hatching. The larvae were reared until adult emergence in plastic beakers (14.5 × 10.5 cm²; five instars per beaker). The requisite stages were taken from the stock culture for experiments.

Slow and fast development on scarce/abundant prey

During the standardization of prey quantity, it was found that early instars, viz. first, second and third instars of *M. sexmaculatus* and *P. dissecta*, consume 6–12 second and third instars of *A. craccivora* per day, while fourth instars and adult males and females consume 10–20 second and third instars of *A. craccivora* per day. The treatments of prey-scarce and prey-abundant conditions were selected on this basis.

Ten pairs of 10-day-old unmated adults of the two ladybirds were paired in separate plastic Petri dishes (size as above) and placed under prey scarce (3–5 second and third instars of *A. craccivora* per day) and prey abundant (25–30 second and third instars of *A. craccivora* per day) conditions. A total of 260 eggs from the first 5 days of oviposition of each ladybird species on each prey quantity were selected. Hatched instars were reared individually in Petri dishes (size as above) on the prey quantity as provided to their parents till adult emergence. They were observed for survival and moulting with all

Table 1. Durations of different life stages of *M. sexmaculatus* and *P. dissecta* on scarce and abundant prey supply.

Prey supply	Ladybird species	Developmental duration (days)					
		First instar	Second instar	Third instar	Fourth instar	Pre-pupa	Pupa
Scarce prey	<i>M. sexmaculatus</i>	2.86 ± 0.07 (B)	1.84 ± 0.09 (B)	2.61 ± 0.05 (B)	3.46 ± 0.09 (B)	2.23 ± 0.13 (B)	3.57 ± 0.15 (B)
	<i>P. dissecta</i>	2.95 ± 0.05 (B)	1.86 ± 0.11 (B)	2.82 ± 0.09 (B)	3.79 ± 0.11 (B)	2.32 ± 0.06 (B)	3.91 ± 0.08 (B)
Abundant prey	<i>M. sexmaculatus</i>	1.61 ± 0.03 (A)	1.19 ± 0.04 (A)	1.20 ± 0.06 (A)	1.43 ± 0.10 (A)	1.14 ± 0.11 (A)	2.23 ± 0.10 (A)
	<i>P. dissecta</i>	1.65 ± 0.02 (A)	1.21 ± 0.09 (A)	1.43 ± 0.10 (A)	1.72 ± 0.13 (A)	1.20 ± 0.08 (A)	2.54 ± 0.12 (A)
<i>F</i> _{Prey supply} (<i>P</i> -value); d.f.		136.51 (0.001); 1, 156	63.92 (0.001); 1, 156	335.66 (0.001); 1, 156	409.34 (0.001); 1, 156	143.98 (0.001); 1, 156	196.79 (0.001); 1, 156
<i>F</i> _{Ladybird species} (<i>P</i> -value); d.f.		0.38 (0.77); 1, 156	0.67 (0.416); 1, 156	13.69 (0.001); 1, 156	19.36 (0.001); 1, 156	0.28 (0.595); 1, 156	25.03 (0.001); 1, 156
<i>F</i> _{Prey supply × Ladybird species} (<i>P</i> -value); d.f.		0.14 (0.707); 1, 156	0.24 (0.625); 1, 156	4.02 (0.047); 1, 156	5.85 (0.002); 1, 156	0.07 (0.790); 1, 156	9.54 (0.001); 1, 156

Two-way ANOVA showing the effects of prey supply, ladybird species and their interaction on durations of different life stages. Values are Mean ± SE. For both ladybird species, upper cases in parentheses represent comparison of means between scarce and abundant prey supply within ladybird species. Values followed by different alphabets show significant differences (*P* < 0.05) among means of developmental durations.

Table 2. Results of test for modality of distribution of developmental durations of *M. sexmaculatus* and *P. dissecta* on scarce and abundant prey supply.

Prey supply	Ladybird species	Distribution statistic
Scarce prey	<i>M. sexmaculatus</i>	D = 0.046, <i>P</i> -value = 0.4947
	<i>P. dissecta</i>	D = 0.012, <i>P</i> -value = 0.156
Abundant prey	<i>M. sexmaculatus</i>	D = 0.0035, <i>P</i> -value = 0.9142
	<i>P. dissecta</i>	D = 0.0043, <i>P</i> -value = 0.6293

observations being conducted twice a day. The instars were grouped as slow and fast developing individuals on the basis of their total developmental period following Mishra & Omkar (2012). Mass of emerging adults was taken 6 h after emergence using an electronic balance. Number of immature survival (number surviving out of total number of eggs), proportion of slow:fast emergence (number of slow or fast developing individuals/total number of individuals emerged) and sex ratio in terms of proportion of females in the population, that is number of females in each developmental type (number of females in slow or fast developing individuals/total number of slow or fast developing individuals) was calculated for both ladybird species on each ladybird-prey supply combination.

Effect of slow-fast development on reproductive attributes

The newly emerged adults of each developmental type, i.e., slow and fast developing individuals, were paired in Petri dishes (size as above) and provided with the prey quantity on which they had completed development. Daily oviposition was recorded for the next 20 days and egg viability was recorded in 10 pairs from each type (i.e., slow and fast) under each ladybird-prey supply combination.

Statistical analysis

Data on total developmental durations (from day of egg laying to adult emergence) for *M. sexmaculatus* and *P. dissecta* on each prey quantity were subjected to Hartigan’s dip test for unimodality in statistical software ‘R’ (version 3.0.1; R Development Core Team, 2013) to assess for type of distribution (unimodal, bimodal or multimodal). In case of non-unimodal statistical value being obtained, the interpretation of bimodality was done in combination with graphical representation. The data were also divided into three groups of fast, intermediate and slow developing individuals, with number of grown-up males and females in each group (table 1). Individuals who had an intermediate duration of development were present in negligible numbers hence excluded from the further analysis.

Chi-square (χ^2) ‘goodness of fit’ analysis was used for the comparison of (i) number of immature survival on scarce and abundant prey supply, (ii) proportion of slow:fast emergence and sex ratio between slow and fast developing individuals on each prey supply and also between scarce and abundant prey supply. When degree of freedom (d.f.) = 1, Yates correction for continuity was employed, while for multiple comparisons, i.e., when d.f. > 1, Bonferroni corrections were made using R software. The data were subjected to two way analysis of variance (ANOVA) taking ladybird species, prey supply (scarce and abundant) as independent factors and durations of different life stages of ladybirds as dependent

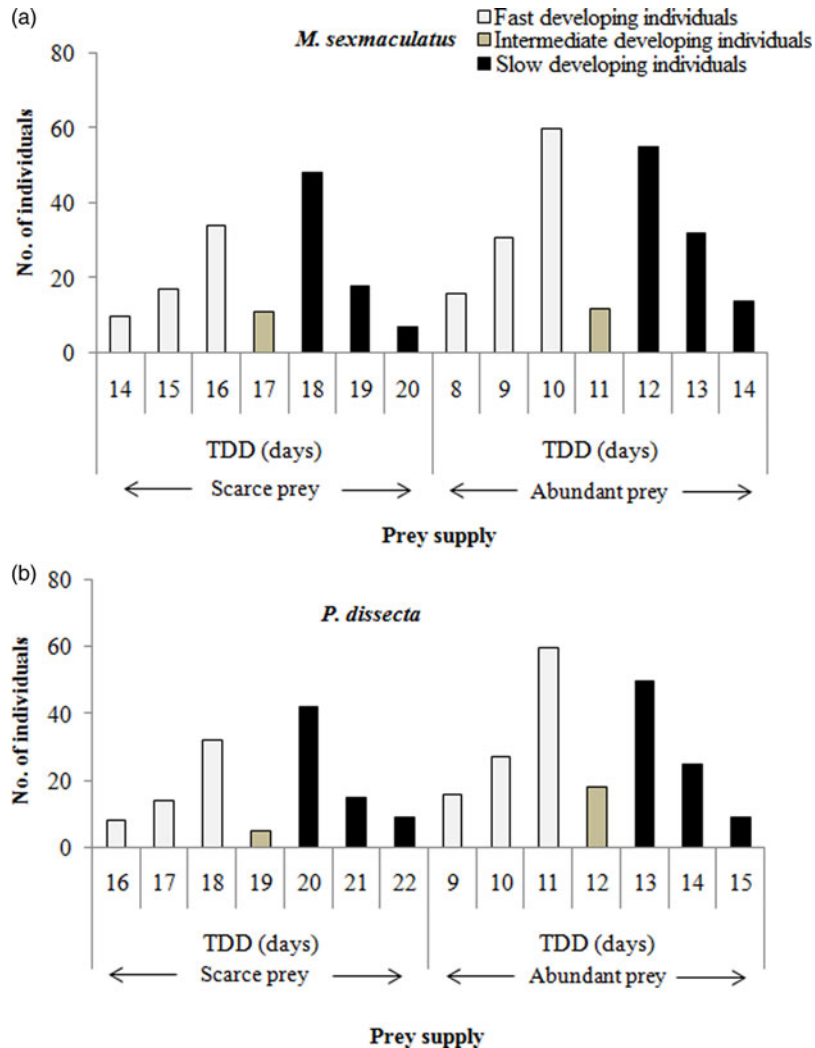


Fig. 1. Frequency distribution of total developmental duration (TDD; in days) of (a) *Menochilus sexmaculatus* and (b) *Propylea dissecta* on scarce and abundant prey supply. Bars indicate number of individuals emerging at each development duration.

factors followed by Tukey's *post hoc* comparison of means. Further the data were again subjected to three way ANOVA taking ladybird species, prey supply (scarce and abundant) and developmental type (slow/fast) as independent factors and total developmental duration as dependent factor followed by Tukey's *post hoc* comparison of means. The data on body mass of males and females taking as dependent factor were subjected to General multivariate analysis of variance (MANOVA) taking ladybird species, prey supply, developmental type and developmental sex as independent factors followed by Tukey's *post hoc* comparison of means. Insignificant interactions ($P > 0.05$) were removed.

The data on adult longevity, fecundity and per cent egg viability (dependent factors) were checked for normal distribution prior to subjecting them to three way ANOVA taking prey supply (scarce and abundant), ladybird species, and developmental type (slow/fast) as independent factors. Differences between means were calculated using Tukey's *post hoc* honest test of significance at 5% levels. All statistical analyses, except χ^2 tests, were performed using MINITAB

15.0. Per cent data were arcsine transformed prior to ANOVA followed by Tukey's *post hoc* comparison of means. Insignificant interactions ($P > 0.05$) were removed.

Results

The overall distribution of developmental durations of *M. sexmaculatus* and *P. dissecta* was not unimodal (table 2) and revealed a clear bimodal pattern when the frequencies of the developmental durations were graphed (fig. 1).

Immature survival of *M. sexmaculatus* ($\chi^2 = 51.70$; $P = 0.001$; d.f. = 1) and *P. dissecta* ($\chi^2 = 53.07$; $P = 0.001$; d.f. = 1) differed significantly with the prey quantity, with higher survival under abundant prey supply (fig. 2). However, the difference in immature survival between ladybird species on each prey supply was not significant (fig. 2).

The proportion of slow:fast emergence was significantly different when beetles were fed on scarce and abundant prey supply (fig. 3a). A comparison of slow developing

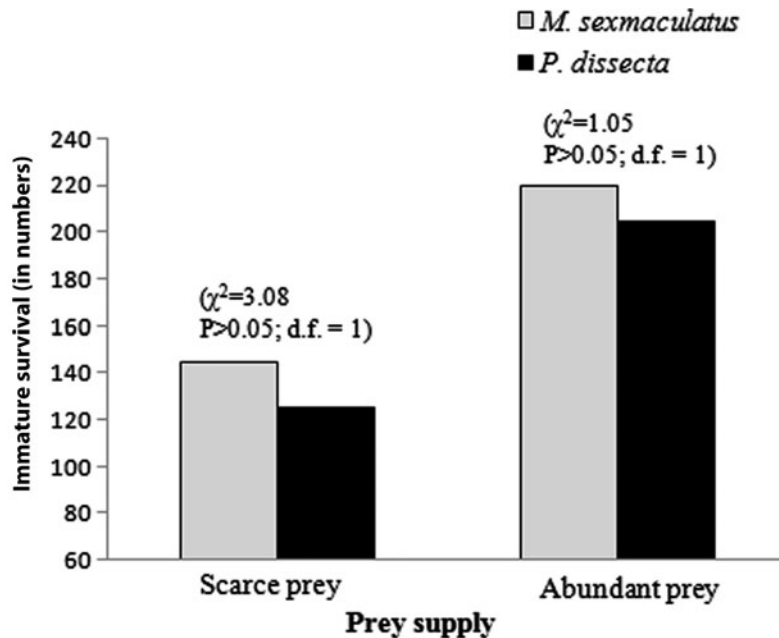


Fig. 2. Immature survival (number surviving out of 260 eggs) of *Menochilus sexmaculatus* and *Propylea dissecta* on scarce and abundant prey supply. χ^2 values present above each set of bars indicate difference between immature survival of each ladybird species on each prey supply.

individuals on scarce and abundant prey supply showed significant differences for *M. sexmaculatus* ($\chi^2 = 19.26$; $P = 0.001$; d.f. = 1) and *P. dissecta* ($\chi^2 = 19.45$; $P = 0.001$; d.f. = 1). Similar significant differences were recorded for fast developing individuals of *M. sexmaculatus* and *P. dissecta*. The number of slow developing individuals was not significantly different between the two ladybirds on scarce ($\chi^2 = 0.12$; $P > 0.05$; d.f. = 1) and abundant ($\chi^2 = 0.23$; $P > 0.05$; d.f. = 1) prey supply. The higher slow developing individuals in both ladybird species were recorded on scarce prey supply and the lower on abundant prey supply (fig. 3a).

The sex ratios of slow and fast developing individuals of *M. sexmaculatus* and *P. dissecta* on scarce and abundant prey supply were significantly different (fig. 3b). The sex ratio was female biased in slow developing individuals of both the ladybirds under both prey supply conditions. The number of slow developing females did not differ significantly between scarce and abundant prey supply in *M. sexmaculatus* ($\chi^2 = 3.93$; $P > 0.05$; d.f. = 1) and *P. dissecta* ($\chi^2 = 2.61$; $P > 0.05$; d.f. = 1). Insignificant differences were recorded for fast developing females in *M. sexmaculatus* ($\chi^2 = 5.57$; $P > 0.05$; d.f. = 1) and *P. dissecta* ($\chi^2 = 5.87$; $P > 0.05$; d.f. = 1). The sex ratio in fast developing individuals of both the species was almost 50:50 on abundant prey supply, but was male biased on scarce prey supply (fig. 3b).

Durations of different life stages of *M. sexmaculatus* and *P. dissecta* varied significantly on scarce and abundant prey supply conditions. *Post hoc* analysis revealed that all the life stages of both the ladybirds took the longest duration to develop on scarce prey supply and shortest on abundant prey supply (table 3). Total developmental duration of slow and fast developing individuals varied significantly between and within prey supply (fig. 4). ANOVA revealed that independent factors, i.e., prey supply ($F = 13.93$, $P = 0.001$, d.f. = 1, 156), ladybird species ($F = 158.13$, $P = 0.001$, d.f. = 1, 156) and

developmental types ($F = 58.72$, $P = 0.001$, d.f. = 1, 156) had significant influence on the total developmental duration. The interactions between prey supply and ladybird species ($F_{\text{interaction}} = 5.85$, $P = 0.002$, d.f. = 1, 156), prey supply and developmental types ($F_{\text{interaction}} = 5.10$, $P = 0.025$, d.f. = 1, 156), and ladybird species and developmental types ($F_{\text{interaction}} = 10.51$, $P = 0.001$, d.f. = 1, 156) were significant.

Body mass of slow and fast developing individuals varied significantly between and within prey supply conditions. Males and females of fast developing individuals were heavier on both prey supplies than slow developing individuals (table 4). Such differences were also prominent between the two sexes within each species, with the females always heavier than the males. *Post hoc* analysis revealed that body mass of males and females of both developmental types was maximum on abundant prey supply and minimum on scarce prey supply. This trend was similar in both species. These results were also supported by ANOVA, which revealed that prey supply, ladybird species, developmental types, developmental sex and their interactions had significant influence on the body mass (table 4).

Adult longevity, fecundity and egg viability of slow and fast developing individuals varied significantly between and within prey supply conditions (table 5). Three-way ANOVA revealed that slow developing adults had higher longevities than the fast developing individuals, while significantly higher numbers of eggs were laid by fast developing individuals with higher per cent egg viability than by slow developing individuals. This trend was similar in both species (table 5).

Discussion

The results indicate the presence of two developmental rates within a cohort of *M. sexmaculatus* and *P. dissecta*, the proportion of which were significantly modified by varying prey quantity. Prey quantity also significantly influenced the

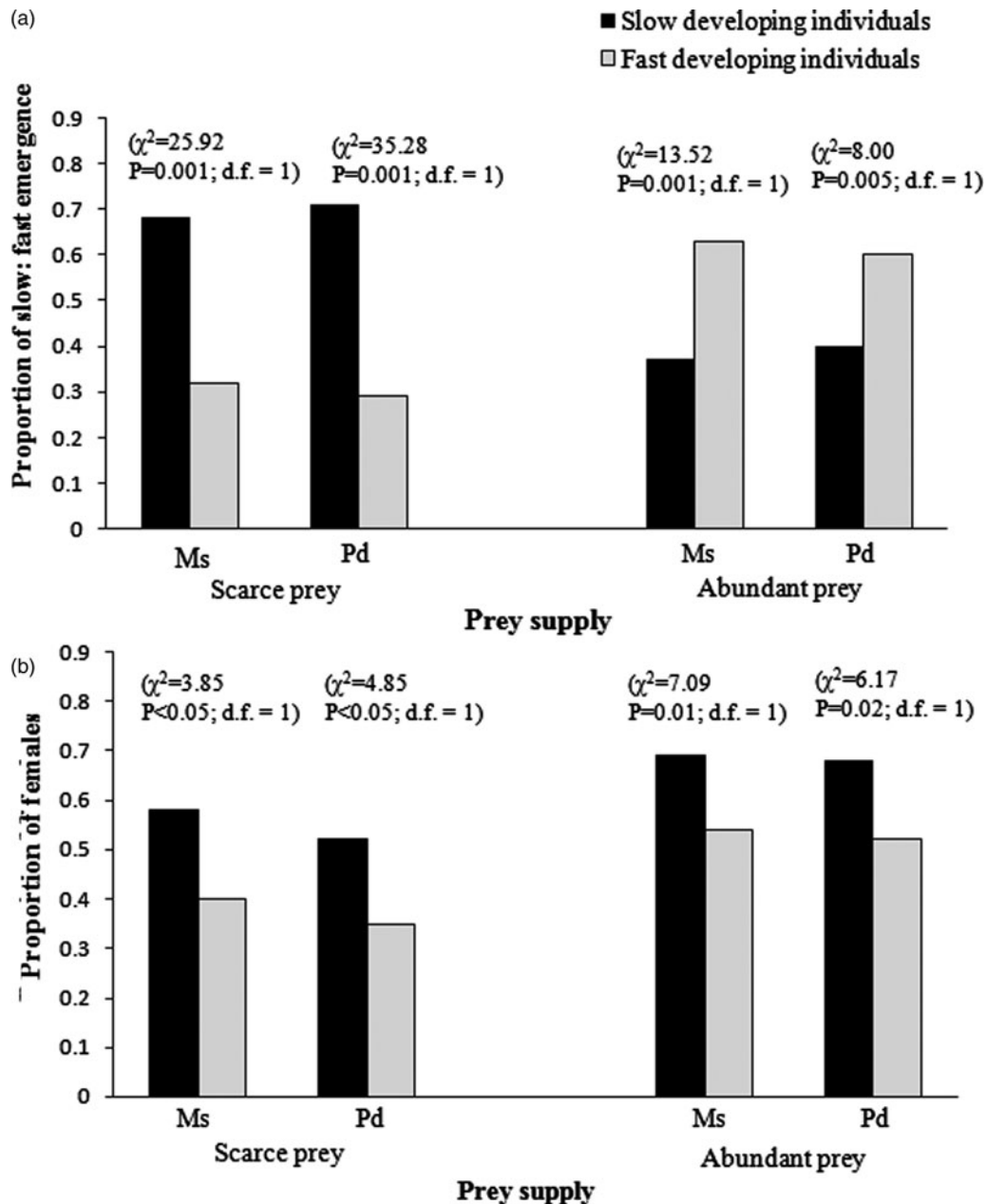


Fig. 3. (a) Proportion of slow:fast emergence and (b) Sex ratio (proportion of females) of *Menochilus sexmaculatus* (Ms) and *Propylea dissecta* (Pd) on scarce and abundant prey supply. χ^2 values (significant at $P < 0.05$) present above each set of bars indicate difference between slow and fast developing individuals of each ladybird species on each prey supply.

developmental duration, survival and reproduction of both the ladybirds. Both developmental types took the longest time to develop under scarce prey conditions and shortest time on abundant prey conditions. Fast developing individuals were heavier than the slow developing ones and their fecundity and egg viability were also highest. Fecundity, egg viability and adult longevity were highest under abundant prey supply.

There exists an inherent variation in developmental rate of *M. sexmaculatus* and *P. dissecta* within a cohort provided with same abiotic and biotic conditions. Such an inherent variation

in developmental rate has also been reported in salmonid fish (Gross, 1985), butterflies, *Maculinea rebeli* (Hirchke) (Schönrogge *et al.*, 2000; Witek *et al.*, 2006) and *Bicyclus anynana* (Butler) (Lewis *et al.*, 2010), predaceous syrphid, *Microdon mutabilis* (L.) (Schönrogge *et al.*, 2000), nematode, *Teladorsagia circumcincta* (Stadelman) (Skorping, 2007) and other insects (Gouws *et al.*, 2011) including ladybirds (Mishra & Omkar, 2012; Singh *et al.*, 2014, 2016; Dixon *et al.*, 2015). Though, not commonly assessed, but in ladybirds this inherent variation in developmental rates within the same cohort and population has been observed (Rodríguez-Saona & Miller, 1995; Dixon,

Table 3. Total developmental duration and number of grown-up males and females of fast, intermediate and slow developmental types of *M. sexmaculatus* and *P. dissecta* on scarce and abundant prey supply.

Prey supply	Ladybird species	Developmental type	Developmental sex	Number of grown-up males and females	Average duration of total development (days)
Scarce prey	<i>M. sexmaculatus</i>	Fast	Males	21	15.76 ± 0.48
			Females	25	16.24 ± 0.37
		Intermediate	Males	4	16.60 ± 0.21
			Females	6	17.40 ± 0.20
		Slow	Males	41	17.08 ± 0.26
			Females	58	18.92 ± 0.30
	<i>P. dissecta</i>	Fast	Males	17	17.59 ± 0.32
			Females	19	18.41 ± 0.35
		Intermediate	Males	7	18.51 ± 0.44
			Females	11	19.49 ± 0.25
		Slow	Males	42	19.36 ± 0.16
			Females	47	20.64 ± 0.33
Abundant prey	<i>M. sexmaculatus</i>	Fast	Males	83	9.71 ± 0.35
			Females	56	10.29 ± 0.25
		Intermediate	Males	5	10.69 ± 0.20
			Females	7	11.31 ± 0.31
		Slow	Males	25	11.39 ± 0.29
			Females	56	12.61 ± 0.25
	<i>P. dissecta</i>	Fast	Males	80	10.33 ± 0.34
			Females	43	11.67 ± 0.22
		Intermediate	Males	2	11.31 ± 0.26
			Females	3	12.69 ± 0.21
		Slow	Males	26	12.29 ± 0.29
			Females	56	13.71 ± 0.27

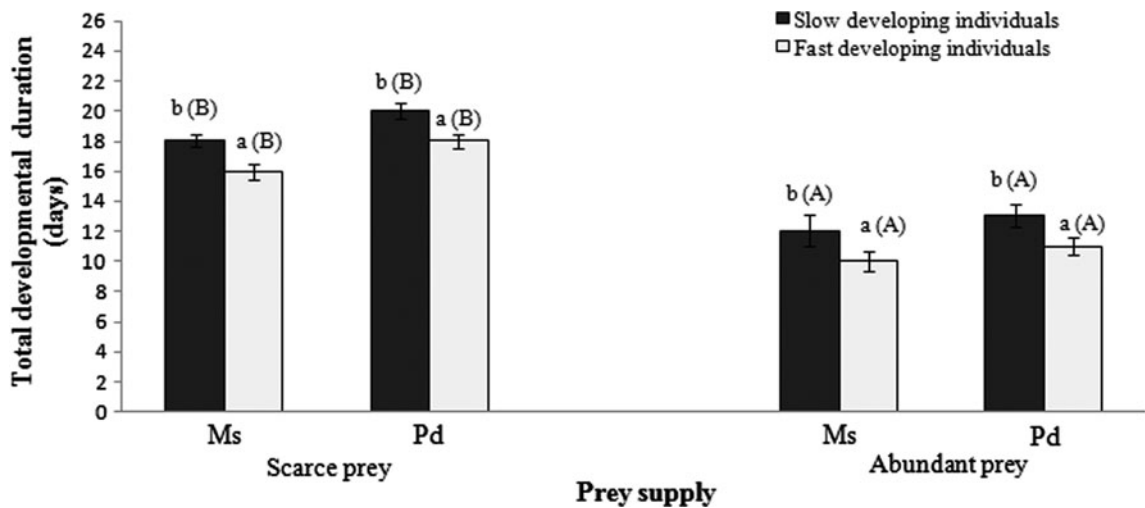


Fig. 4. Total developmental duration of *Menochilus sexmaculatus* (Ms) and *Propylea dissecta* (Pd) on scarce and abundant prey supply. Values are Mean ± SE. For both ladybird species, lower cases represent comparison of means between slow and fast developing individuals within ladybird species on each prey supply, and upper cases in parentheses represent comparison of means between slow and fast developing individuals within ladybird species on scarce and abundant prey supply. Values followed by different alphabets show significant differences ($P < 0.05$) among means of slow and fast developing individuals.

2000; Mishra & Omkar, 2012; Singh *et al.*, 2014, 2016; Dixon *et al.*, 2015), albeit their distribution pattern has not been assessed until recently (Mishra & Omkar, 2012; Singh *et al.*, 2014, 2016; Dixon *et al.*, 2015). The lack of unanimity about bimodality of developmental durations of ladybirds could simply be a result of very few studies on their growth and development attempting to assess the distribution of development rates.

One of the probable reasons behind the provisioning of slow and fast developing eggs by the female in an egg batch could be to minimize local extinction by catastrophic events as suggested by the bet-hedging hypothesis (Hanski, 1988). Other possible rationales behind the variation in developmental rate could be: (a) disparity in maternal investment (Osawa, 2003), (b) asynchronization in hatching (Kawai, 1978; Osawa, 1992), (c) eggs with different metabolic rates due to allelic

Table 4. Body mass of males and females of slow and fast developmental types of *M. sexmaculatus* and *P. dissecta* on scarce and abundant prey supply.

Prey supply	Ladybird species	Developmental type	Developmental sex	Body mass of males and females (mg)	
Scarce prey	<i>M. sexmaculatus</i>	Slow	Males	8.31 ± 0.32 ^{a A (A)}	
			Females	10.68 ± 0.28 ^{b A (A)}	
		Fast	Males	10.13 ± 0.36 ^{a B (A)}	
			Females	11.82 ± 0.41 ^{b B (A)}	
		<i>P. dissecta</i>	Slow	Males	8.77 ± 0.22 ^{a A (A)}
	Females			10.53 ± 0.17 ^{b A (A)}	
	Fast		Males	9.54 ± 0.25 ^{a B (A)}	
			Females	11.30 ± 0.34 ^{b B (A)}	
	Abundant prey		<i>M. sexmaculatus</i>	Slow	Males
		Females			13.42 ± 0.28 ^{b A (B)}
Fast		Males		14.36 ± 0.41 ^{a B (B)}	
		Females		16.22 ± 0.39 ^{b B (B)}	
<i>P. dissecta</i>		Slow		Males	12.17 ± 0.46 ^{a A (B)}
			Females	13.84 ± 0.50 ^{b A (B)}	
		Fast	Males	13.65 ± 0.44 ^{a B (B)}	
			Females	15.48 ± 0.23 ^{b B (B)}	
		$F_{\text{Prey supply}}$ (<i>P</i> -value); d.f.			
$F_{\text{Ladybird species}}$ (<i>P</i> -value); d.f.				54.41 (0.001); 1, 156	
$F_{\text{Developmental types}}$ (<i>P</i> -value); d.f.				37.32 (0.001); 1, 156	
$F_{\text{Developmental sex}}$ (<i>P</i> -value); d.f.				46.35 (0.001); 1, 156	
$F_{\text{Prey supply} \times \text{ladybird species}}$ (<i>P</i> -value); d.f.				31.11 (0.001); 1, 156	
$F_{\text{Prey supply} \times \text{developmental types}}$ (<i>P</i> -value); d.f.				15.19 (0.001); 1, 156	
$F_{\text{Prey supply} \times \text{developmental sex}}$ (<i>P</i> -value); d.f.				7.61 (0.002); 1, 156	
$F_{\text{Ladybird species} \times \text{developmental types}}$ (<i>P</i> -value); d.f.				21.33 (0.001); 1, 156	
$F_{\text{Ladybird species} \times \text{developmental sex}}$ (<i>P</i> -value); d.f.				10.54 (0.001); 1, 156	
$F_{\text{Developmental types} \times \text{developmental sex}}$ (<i>P</i> -value); d.f.				3.85 (0.010); 1, 156	

General MANOVA showing the effects of prey supply, ladybird species, developmental types, developmental sex and their interactions on body mass of males and females.

Values are Mean ± SE.

For both ladybird species, lower cases represent comparison of means between males and females within slow/fast developing individuals within ladybird species on each prey supply, upper cases represent comparison of means between males of slow and fast developing individuals within ladybird species on each prey supply and females of slow and fast developing individuals within ladybird species on each prey supply, upper cases in parentheses represent comparison of means between males of slow/fast developing individuals within ladybird species on scarce and abundant prey supply and females of slow/fast developing individuals within ladybird species on scarce and abundant prey supply.

Values followed by different alphabets show significant differences ($P < 0.05$) among means of slow and fast developing individuals.

differences (Sloggett & Lorenz, 2008; Osawa & Ohashi, 2008), and/ or (d) mother laying eggs with different sizes and nutritional content (Hodek *et al.*, 2012). High metabolic rate is linked with short developmental period and high fecundity (Marinkovic *et al.*, 1986; Hoffmann & Parsons, 1989) whereas the low metabolic rate is known to increase longevity and stress resistance (Service, 1987; Hoffmann & Parsons, 1989). Egg size also affects development success, developmental rate, offspring size and fecundity in insects (Tauber *et al.*, 1991; Fox & Czesak, 2000).

The proportion of slow:fast emerged individuals differed notably with varying prey supply. The reduced rates of prey consumption may be a key factor for slow development and high mortality of both larvae and adults (Phoofolo *et al.*, 2008). The prey intake, its digestibility and utilization significantly influence the growth, developmental time, body biomass and survival of ladybirds (Rath, 2010). It is likely that on abundant prey supply, fast developing individuals were able to develop better and were present in higher numbers, whereas slow developing individuals were found in higher numbers on scarce prey supply possibly owing to decreased availability of nutrients. Such strained nutritive conditions would not be suitable for fast developing individuals, thus causing high mortality and leading to a skewed ratio in favour of slow developing individuals. Also evolutionary theory illustrates that fast

development occurs under suitable conditions and slow development occurs under adverse conditions (e.g., Davidowitz & Nijhout, 2004; Stillwell *et al.*, 2007, 2010; Chown & Gaston, 2010). Additionally, faster-growing individuals are expected to be more sensitive to starvation because of their need for higher metabolic rates. Hence, difference in metabolic rate might also be responsible for this skewed ratio. It has been reported earlier that ectotherm species reared under stressful environments (i.e., food and water stress) have lower metabolic rates than related species from more benign environments (Juliano, 1986). We believe that the differing slow and fast ratio found under differing prey supply indicates the increased mortality of a particular development type as they could not reach the minimum threshold mass for achieving the next developmental stage under each prey supply.

The fecundity of both slow and fast developing individuals of *M. sexmaculatus* and *P. dissecta* was low under scarce prey supply, which can be attributed to decreased nutrient resources restricting the development and reproduction of the ladybirds (Moczek, 1998; O'Brien *et al.*, 2005; Hodek *et al.*, 2012). Furthermore, Reznik & Vaghina (2013) reported that nutrients (quality and quantity of prey) affect the rate of reproductive maturation and fecundity in *H. axyridis*. Prey scarcity is known to affect fitness of the developing life stages (Agarwala *et al.*, 2001; Stamp, 2001), the development of

Table 5. Adult longevity, fecundity and egg viability of slow and fast developmental types of *M. sexmaculatus* and *P. dissecta* on scarce and abundant prey supply

Prey supply	Ladybird species	Developmental type	Adult longevity (days)	Fecundity (number of eggs)	Egg viability (%)
Scarce prey	<i>M. sexmaculatus</i>	Slow	43.11 ± 0.45 ^{b (A)}	323.25 ± 38.89 ^{a (A)}	62.93 ± 1.32 ^{a (A)}
		Fast	39.40 ± 0.55 ^{a (A)}	467.70 ± 50.16 ^{b (A)}	66.20 ± 1.47 ^{b (A)}
	<i>P. dissecta</i>	Slow	41.65 ± 1.14 ^{b (A)}	204.30 ± 20.65 ^{a (A)}	55.29 ± 1.58 ^{a (A)}
		Fast	37.29 ± 0.62 ^{a (A)}	259.27 ± 16.62 ^{b (A)}	57.51 ± 1.37 ^{b (A)}
Abundant prey	<i>M. sexmaculatus</i>	Slow	70.10 ± 0.87 ^{b (B)}	1087.80 ± 32.61 ^{a (B)}	85.40 ± 1.31 ^{a (B)}
		Fast	66.03 ± 0.78 ^{a (B)}	1128.60 ± 28.90 ^{b (B)}	89.02 ± 1.12 ^{b (B)}
	<i>P. dissecta</i>	Slow	65.19 ± 0.72 ^{b (B)}	856.00 ± 30.40 ^{a (B)}	80.36 ± 2.75 ^{a (B)}
		Fast	63.42 ± 0.29 ^{a (B)}	902.40 ± 36.32 ^{b (B)}	83.38 ± 1.70 ^{b (B)}
$F_{\text{Prey supply}}$ (P -value); d.f.			228.19 (0.001); 1, 156	174.42 (0.001); 1, 76	87.29 (0.001); 1, 76
$F_{\text{Ladybird species}}$ (P -value); d.f.			43.17 (0.001); 1, 156	77.58 (0.001); 1, 76	10.78 (0.002); 1, 76
$F_{\text{Developmental types}}$ (P -value); d.f.			5.22 (0.024); 1, 156	61.07 (0.001); 1, 76	25.76 (0.001); 1, 76
$F_{\text{Prey supply} \times \text{ladybird species}}$ (P -value); d.f.			22.96 (0.001); 1, 156	3.86 (0.003); 1, 76	31.27 (0.001); 1, 76
$F_{\text{Prey supply} \times \text{developmental types}}$ (P -value); d.f.			9.64 (0.001); 1, 156	18.27 (0.001); 1, 76	9.60 (0.001); 1, 76
$F_{\text{Ladybird species} \times \text{developmental types}}$ (P -value); d.f.			3.85 (0.004); 1, 156	9.51 (0.001); 1, 76	6.70 (0.012); 1, 76

Three-way ANOVA showing the effects of prey supply, ladybird species, developmental types and their interactions on adult longevity, fecundity and egg viability.

Values are Mean ± SE.

For both ladybird species, lower cases represent comparison of means between slow and fast developing individuals within ladybird species on each prey supply, and upper cases in parentheses represent comparison of means between slow and fast developing individuals within ladybird species on scarce and abundant prey supply.

Values followed by different alphabets show significant differences ($P < 0.05$) among means of a slow and fast developing individuals.

ovarioles (Hodek *et al.*, 2012) and even resorption of eggs (Cope & Fox, 2003; Omkar & Pervez, 2003).

In cohorts of *M. sexmaculatus* and *P. dissecta*, fast developing individuals were large in size and females were more fecund with higher egg viability than slow developing individuals in both prey supply. Dixon *et al.* (2015) reported that the adult weights of the fast-developing individuals were greater than that of slow-developing individuals when reared on an excess of aphids per day. The variation in fecundity was supported by the differences in body mass (Darwin, 1874). Larger females lay more and bigger eggs (Stearns, 1992; Charnov & Ernest, 2006; Davidowitz, 2008) and these are considered to facilitate faster development (Garcia-Barros, 2000; Katvala & Kaitala, 2001; Roff, 2002; Omkar & Afaq, 2013). Also, the higher fecundity and decreased longevity of fast developing females indicate possible trade-off between reproduction and survival whereas slow developing individuals conserve nutrient reserves for somatic maintenance leading to low energy availability, slower growth, delayed sexual maturation, low gonadal steroid production, small adult body size and low fecundity (Kuzawa, 2005, 2008; Walker *et al.*, 2006). The higher per cent egg viability in the fast developing individuals may be ascribed to larger size of males that possibly supply higher ejaculate, better quality of genes in addition to accessory gland proteins (Avila *et al.*, 2011; Helinski & Harrington, 2011). Lewis *et al.* (2010) reported that the slow developing males were smaller in size, produced fewer fertile sperm and longer time to mate as compared with fast developing ones.

Besides numerous benefits of fast developing individuals, slow developing individuals were found to be superior when food resources were scarce (Sevenster & Van Alphen, 1993). This may also act as a counterbalancing force that preserves the slow developing individuals in the population. Dixon *et al.* (2015) reported that the optimum growth rate of a predator is positively associated with that of its prey and that plays a crucial role in evolution. The variation in responses with change in prey is similar to that witnessed in these two

ladybirds at varying temperatures under *ad libitum* prey supply (Singh *et al.*, 2014, 2016). Which of the two factors has a stronger influence in determining the slow and fast developers ratio as well as their physiological responses is not yet clear and would be better determined through a nested experimental design. Theoretically, temperature should have a greater influence as even minor shifts are known to cause prominent developmental variations.

The adaptive significance of the existence of slow and fast development in the populations of *M. sexmaculatus* and *P. dissecta* could be that in sub-tropical countries like India where almost all seasons are present and aphid availability in ecosystem fluctuates; this developmental rate polymorphism help in maintaining the populations of the individuals even under unsuitable environmental conditions, like prey scarcity.

The present study indicates that: (i) slow and fast developing individuals exist under both scarce and abundant prey supply in *M. sexmaculatus* and *P. dissecta*; (ii) slow:fast ratio changes with prey supply and followed a similar trend in both ladybirds; (iii) more fast developing individuals were recorded on abundant prey supply, and less on scarce prey supply; (iv) slow developing individuals showed a female biased sex ratio with increased longevities on both prey supply; (v) fast developing individuals were almost heavier than the slow developing individuals; (vi) selection for faster development leads to higher fitness due to increased fecundity and per cent egg viability. The likely improvement in fecundity of fast developers indicates it to be a genetic trait possibly conserved across ladybird species, which could help in the selection of fast developing lines for their application in biocontrol of insect pests.

Acknowledgements

Neha Singh and Omkar are thankful to the Department of Higher Education, Govt. of U.P., Lucknow, India for providing financial assistance under the Centre of Excellence programme for this work. Geetanjali Mishra is thankful to the

Department of Science and Technology, New Delhi, India for financing a project on the topic under the Fast Track Young Scientist Scheme.

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