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PREY SPECIES MEDIATED SLOW AND FAST DEVELOPMENT IN TWO APHIDOPHAGOUS LADYBIRD BEETLES

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ABSTRACT

Extensive research has explored how environmental factors impact the developmental rates of various organisms. However, the phenomenon of developmental rate polymorphism, where individuals within a cohort exhibit either slow or fast developmental rates under fluctuating environmental conditions, remains underexplored. In current study, we investigated how different prey species (*Aphis craccivora* Koch, *Aphis gossypii* Glover, *Aphis nerii* Boyer de Fonscolombe, *Lipaphis erysimi* (Kaltenbach) and *Rhopalosiphum maidis* (Fitch)) affect the slow and fast development rates of two ladybird species, *Cheilomenes sexmaculata* (Fabricius) and *Propylea dissecta* (Mulsant), and how these rates influence their reproductive traits. We observed a distinct bimodal distribution pattern for each prey species, with two peaks representing the fast and slow developers, respectively. The distribution was skewed depending on the type of prey. Slow developers had a higher proportion of females, lived longer, and had lower body mass. On the other hand, fast-developing females had higher fecundity and egg viability. We observed a higher frequency of slow developers among beetles fed on *A. nerii, L. erysimi,* and *R. maidis* and fewer on *A. craccivora* and *A. gossypii*. We hypothesised that the observed variation in developmental rates at emergence is due to selective mortality influenced by the prey species, rather than differences in the developmental rates at egg laying. This study lays the groundwork for further research into developmental rate polymorphism, enhancing our understanding of its ecological and evolutionary causes, and aiding in the selection of fast developing bioagents for biological pest control.

KEY WORDS: Coleoptera, bimodal distribution, developmental duration, slow: fast emergence, sex ratio, body mass, fecundity

INTRODUCTION

The development of an individual is influenced by both genetic and environmental factors. According to Stern (2010), the connection between development and physiology aids in the conversion of genotypes into phenotypes and is likely to have significant effects on evolutionary outcomes. Numerous studies have documented species-to-species variations in developmental rates in response to a variety of environmental factors (Plaistow *et al*., 2005; Stillwell *et al*., 2007, 2010; Chown & Gaston, 2010) in different insects such as *Drosophila melanogaster* Meigen (Partridge & Fowler, 1992), the lepidopteran *Manduca sexta* (L.). In addition, in other organisms, genetic variations in phenotypic plasticity for developmental rates and size in sub-populations have been used to select organisms that develop faster (D'Amico *et al*., 2001). Since somatic growth and reproductive development occur simultaneously in developing instars and are both affected by changes in the rearing environment, developmental rates can also be used to predict future fecundity (Awmack & Leather, 2007). According to Oli (2004), rapidly developing populations are less sensitive to changes in survival rates but more sensitive to changes in reproductive parameters.

Salmonid fish (Gross, 1985), butterflies, *Maculinea rebeli* (Hirchke), and many other taxa have all exhibited two distinct rates of development within a cohort (Thomas *et al*., 1998; Nowicki *et al*., 2005; Witek *et al*., 2006). Developmental rate is also known to affect sperm quality as per the studies in *Bicyclus anynana* (Lewis *et al*., 2010) where it has been reported that the faster developing males produce less non-fertile sperm as compared to the slow developing males. Most organisms, including the ladybird *Adalia bipunctata* L., probably exhibit subtle variations

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(Dixon, 2000).

In two species of ladybirds, *Cheilomenes sexmaculata* (Fabricius) and *Propylea dissecta* (Mulsant) (Mishra & Omkar, 2012; Singh *et al.*, 2014), and *Zygogramma bicolorata* Pallister, a chrysomelid (Pandey *et al.*, 2013), this difference in development was investigated and formally reported. Both intraspecific body size and developmental rates have been found to have such a bimodal distribution. Social insects have a larger variation in size than non-social insects, but it is not completely absent (Gouws *et al.*, 2011). The bimodal distribution of the ladybirds, *C. sexmaculata* and *P. dissecta* has been found to shift with temperature in both species. It has been found to shift with change in temperatures; more slow developers arise at lower temperatures (15 and 20°C) and less at higher ones (30 and 35°C) with a 50:50 slow: fast distribution at 25°C, being an optimal temperature (Singh *et al.*, 2014). The change in the proportion of slow: fast emergence was attributed to selective mortality influenced by the different temperatures.

It has been demonstrated that the prey species influences growth, development, survival, mortality, and reproduction in aphidophagous ladybirds (Arijs & De Clercq, 2004; Omkar & Bind, 2004; Omkar & James, 2004; Omkar & Mishra, 2005; Nyaanga *et al.*, 2012; Williams & Flaxman, 2012). This influence may be due to (a) the ephemeral nature of aphid colonies (Osawa, 2000; Van der Werf *et al.*, 2000) (b) prey quality (Pervez & Omkar, 2004; Omkar & Mishra, 2005; Omkar *et al.*, 2009; Omkar *et al.*, 2011; Bista *et al.*, 2012), and (c) prey quantity (Francis *et al.*, 2000; Omkar *et al.*, 2010). High quality prey supports better development and growth with lower, whereas poor quality prey has the opposite effect (Chen *et al.*, 2012). Ladybirds' immature development and reproductive output are also affected by food scarcity (Omkar & Pervez, 2003; Agarwala *et al.*, 2008; Phoofolo *et al.*, 2008, 2009; Santos-Cividanes *et al.*, 2011).

We chose to examine how different prey species affect the slow and fast development of two locally common aphidophagous ladybirds, given the significant impact that food has on their development. We hypothesised that the ratio of slow to fast developers would fluctuate with changes in biotic factors such as prey quality. Specifically, we anticipated that poor quality prey would lead to a higher proportion of slower developers, while high quality prey would favor faster development. This study aims to identify the differential rates of development in ladybirds. By doing so, it will help us understand how ecological and evolutionary changes influence the diversity of life histories. Furthermore, the research is expected to identify ladybird strains with rapid development potential, which could be utilised in biocontrol efforts against various insect pests.

MATERIALS AND METHODS

Insects

Two locally abundant predaceous ladybirds, *C. sexmaculata* and *P. dissecta,* were selected for the study due to (a) their fast development, (b) high reproductive rates, and (c) previous research on related aspects (Mishra & Omkar, 2012; Singh *et al.*, 2014).

Stock Maintenance

Adults of *C. sexmaculata* 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 cm^2) containing daily replenished aphids*, Aphis craccivora* Koch (on host plant *Vigna unguiculata* (L.) taken from polyhouse cultures; 25±2ºC; 65±5% R.H.) under standard laboratory conditions (27±1ºC; 65±5% R.H.; 14L: 10D) in BOD incubators (Yorco Super Deluxe, YSI-440, New Delhi, India). Eggs laid were collected every 24 hours and incubated under the above abiotic conditions until hatching. The larvae were reared until adult emergence in plastic beakers (14.5×10.5 cm^2; 5 larvae per beaker). The requisite stages were taken from the stock culture for experiments.

Experimental Design

(A) Slow and fast development on different prey species

Ten pairs of 10-day-old unmated adults were paired in separate plastic Petri dishes (size as above) and provided

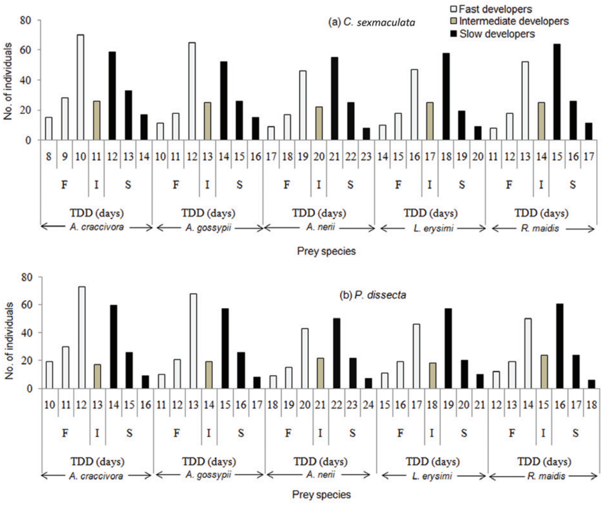

Fig. 1: Frequency distribution of total developmental duration (TDD; in days) of (a) *Cheilomenes sexmaculata* and (b) *Propylea dissecta* on different prey species; where F, I and S represent fast, intermediate and slow developers, respectively. Bars indicate number of individuals emerging at each development duration.

Table 1: Normality of developmental duration of *Cheilomenes sexmaculata* and *Propylea dissecta* on different prey species; where D+, D- and D represents D maximum, minimum and critical, respectively

Prey species	Ladybird species	Normality of data
A. craccivora	*C. sexmaculata*	D+: 0.075 D-: 0.078 D : 0.078; P-Value < 0.01
	P. dissecta	D+: 0.064 D-: 0.067 D : 0.067 ; P-Value: 0.037
A. gossypii	*C. sexmaculata*	D+: 0.081 D-: 0.078 D : 0.081 ; P-Value: 0.019
	P. dissecta	D+: 0.094 D-: 0.086 D : 0.094; P-Value < 0.01
A. nerii	*C. sexmaculata*	D+: 0.069 D-: 0.077 D : 0.077; P-Value: 0.036
	P. dissecta	D+: 0.076 D-: 0.083 D : 0.083; P-Value: 0.040
L. erysimi	*C. sexmaculata*	D+: 0.321 D-: 0.169 D : 0.321; P-Value: 0.023
	P. dissecta	D+: 0.088 D-: 0.062 D : 0.088; P-Value < 0.01
R. maidis	*C. sexmaculata*	D+: 0.078 D-: 0.072 D : 0.078; P-Value < 0.01
	P. dissecta	D+: 0.076 D-: 0.079 D : 0.079; P-Value: 0.027

Table 2: Reproductive attributes of slow and fast developmental types of *Cheilomenes sexmaculata* and *Propylea dissecta* on different prey species. General Linear Model showing the effects of prey species, ladybird species, developmental types and their interactions on fecundity and egg viability

Prey species	Ladybird species	Developmental types	Fecundity (no. of eggs)	Egg viability (%)
A. craccivora	*C. sexmaculata*	Slow	1018.31±32.04$^{a\,(E)}$	90.17±0.62$^{a\,(E)}$
		Fast	1117.80±48.10$^{b\,(E)}$	92.79±0.46$^{b\,(E)}$
	P. dissecta	Slow	786.50±33.24$^{a\,(E)}$	88.55±0.48$^{a\,(E)}$
		Fast	856.11±29.08$^{b\,(E)}$	91.40±0.61$^{b\,(E)}$
A. gossypii	*C. sexmaculata*	Slow	905.21±35.64$^{a\,(D)}$	85.46±0.78$^{a\,(D)}$
		Fast	1016.90±42.44$^{b\,(D)}$	89.32±0.82$^{b\,(D)}$
	P. dissecta	Slow	677.11±28.14$^{a\,(D)}$	83.84±0.65$^{a\,(D)}$
		Fast	750.23±30.26$^{b\,(D)}$	87.45±0.87$^{b\,(D)}$
A. nerii	*C. sexmaculata*	Slow	295.55±22.27$^{a\,(A)}$	59.17±0.82$^{a\,(A)}$
		Fast	348.25±15.09$^{b\,(A)}$	63.59±0.96$^{b\,(A)}$
	P. dissecta	Slow	153.40±23.37$^{a\,(A)}$	54.43±0.84$^{a\,(A)}$
		Fast	214.27±20.76$^{b\,(A)}$	57.35±0.62$^{b\,(A)}$
L. erysimi	*C. sexmaculata*	Slow	509.55±47.59$^{a\,(B)}$	64.98±0.83$^{a\,(B)}$
		Fast	673.83±32.26$^{b\,(B)}$	72.32±0.76$^{b\,(B)}$
	P. dissecta	Slow	414.10±22.65$^{a\,(B)}$	60.53±0.81$^{a\,(B)}$
		Fast	486.20±29.22$^{b\,(B)}$	67.08±0.97$^{b\,(B)}$
R. maidis	*C. sexmaculata*	Slow	816.70±29.09$^{a\,(C)}$	82.18±0.73$^{a\,(C)}$
		Fast	906.00±32.26$^{b\,(C)}$	85.32±0.46$^{b\,(C)}$
	P. dissecta	Slow	506.10±24.17$^{a\,(C)}$	80.18±0.82$^{a\,(C)}$
		Fast	571.80±22.20$^{b\,(C)}$	83.59±0.46$^{b\,(C)}$
		$F_{\text{Prey species}}$ (P-value); df	371.74 (0.001); 4, 380	261.40 (0.001); 4, 380
		$F_{\text{Ladybird species}}$ (P-value); df	117.55 (0.001); 1, 380	469.25 (0.001); 1, 380
		$F_{\text{Developmental types}}$ (P-value); df	105.85 (0.001); 1, 380	171.25 (0.001); 1, 380
		$F_{\text{Prey species x Ladybird species}}$ (P-value); df	155.94 (0.001); 4, 380	20.62 (0.001); 4, 380
		$F_{\text{Prey species x Developmental types}}$ (P-value); df	12.74 (0.001); 4, 380	3.19 (0.014); 4, 380
		$F_{\text{Ladybird species x Developmental types}}$ (P-value); df	36.66 (0.001); 1, 380	2.87 (0.044); 1, 380
		$F_{\text{Prey species x Ladybird species x Developmental types}}$ (P-value); df	11.89 (0.001); 4, 380	7.17 (0.001); 4, 380

Values are Mean±SE.

For both ladybird species, lower cases represent comparison of means between slow and fast development within ladybird species on each prey species, and upper cases in parentheses represent comparison of means between slow and fast development within ladybird species on different prey species.

Values followed by different alphabets show significant differences (P<0.05) amongst means of a slow and fast development.

with one of the five prey species, *viz*. *A. craccivora* from *Dolichos lablab* L.*,* *Aphis gossypii* Glover from *Lagenaria vulgaris* Seringe.*,* *Aphis nerii* Boyer de Fonscolombe from *Calotropis procera* (Aiton)*,* *Lipaphis erysimi* (Kaltenbach) from *Brassica campestris* L. and *Rhopalosiphum maidis* (Fitch) from *Zea mays* L. Three hundred eggs from the first five days of oviposition of each ladybird species on each prey type were selected. Hatched larvae were reared individually in Petri dishes (size as above) on the same prey species as provided to their parents until adult emergence. They were observed for survival and moulting. The larvae were provided with second and third instars of their respective prey @ 30 mg for the first (L_1) and second instars (L_2) and @ 50 mg for the third (L_3) and fourth instars (L_4) and adults. The aphid quantity provided to each instar was intentionally excessive (as confirmed through laboratory testing) because the amount of food is known to affect development (Hodek *et al*., 2012) and the proportion of infertile eggs laid (Perry & Roitberg, 2005). The instars were grouped as slow and fast developers based on their total developmental period, following the methodology of Mishra & Omkar (2012). The body of emerging adults was measured 6 hours after emergence using an electronic balance (Sartorius CP225-D; 0.01 mg precision). For each ladybird-prey combination, the following metrics were calculated separately for slow and fast developers: (1) the immature survival rate (number of individuals surviving out of the total number of eggs), (2) the proportion of slow to fast developers (number of slow or fast developers / total number of individuals emerged), and (3) the sex ratio within each developmental type (number of females among slow or fast developers / total number of slow or fast developers).

(B) Effect of slow-fast development on reproductive attributes

The 10-day old adults of both slow and fast developers (n=20 pairs) of both species of ladybirds were paired in Petri dishes (size as above) and provided with the same prey species on which they had completed development. Once the mating was completed (adults naturally dislodged), females were separated and kept in new Petri dishes with *ad libitum* food. Daily oviposition and percent egg viability was recorded for the next 20 days in 20 pairs from each type (*i.e.* slow and fast) under each ladybird-prey combination. Longevity of adults was also recorded for both the species reared on different prey species.

Statistical analysis

Data for total developmental durations (from the day of egg laying to adult emergence) for *C. sexmaculata* and *P. dissecta* on each prey species were subjected to a Kolomogorov-Smirnov test of normality to assess for a normal distribution. The overall distribution of developmental durations of *C. sexmaculata* and *P. dissecta* was non-normal (Table 1). The developmental duration frequencies were plotted, revealing a distinct bimodal pattern (Fig. 1). Based on the graphical representation, data were divided into two groups of slow and fast developers, with intermediate rate developers present between the fast and slow peaks.

A chi-square 'goodness of fit' analysis was used for the comparison of (i) the number of immature survival on different prey species, (ii) the proportion of slow: fast emergence and sex ratio between slow and fast developers of each prey species and also between each prey species.

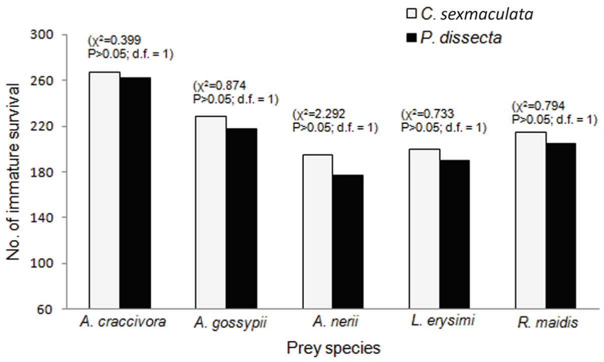

Fig. 2: Immature survival (number surviving out of 300 eggs) of *Cheilomenes sexmaculata* and *Propylea dissecta* on different prey species. Chi-square values present above each set of bars indicate difference between immature survival of each ladybird species on each prey species.

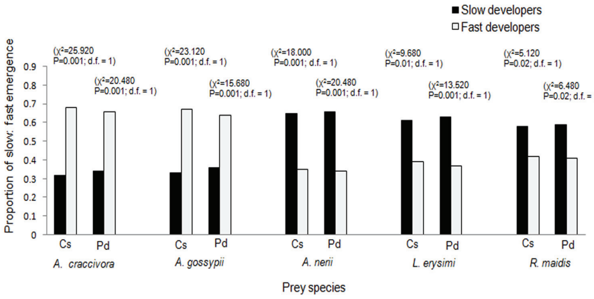

Fig. 3: Graphs depicting proportion of slow: fast emergence of *Cheilomenes sexmaculata* (Cs) and *Propylea dissecta* (Pd) under slow/fast development on different prey species. Chi-square values (significant at P<0.05) present above each set of bars indicate difference between slow and fast developers of each ladybird species on each prey species.

Table 3: Body mass and longevity of slow and fast developmental types of *Cheilomenes sexmaculata* and *Propylea dissecta* on different prey species. General Linear Model showing the effects of prey species, ladybird species, developmental types and their interactions on body mass of adults and adult longevity

Prey species	Ladybird species	Developmental types	Body mass of adults (mg)	Adult Longevity (days)
A. craccivora	*C. sexmaculata*	Slow	13.04±0.53$^{a\,(D)}$	70.13±1.45$^{b\,(D)}$
		Fast	15.65±0.28$^{b\,(D)}$	66.04±0.92$^{a\,(D)}$
	P. dissecta	Slow	14.36±0.27$^{a\,(E)}$	65.22±0.84$^{b\,(D)}$
		Fast	15.49±0.49$^{b\,(D)}$	63.62±0.33$^{a\,(E)}$
A. gossypii	*C. sexmaculata*	Slow	11.03±0.56$^{a\,(C)}$	61.82±1.54$^{b\,(C)}$
		Fast	14.71±0.48$^{b\,(C)}$	59.03±0.68$^{a\,(C)}$
	P. dissecta	Slow	12.74±0.63$^{a\,(D)}$	59.12±1.63$^{b\,(C)}$
		Fast	15.07±0.59$^{b\,(D)}$	55.26±0.60$^{a\,(D)}$
A. nerii	*C. sexmaculata*	Slow	7.03±0.36$^{a\,(A)}$	47.11±0.48$^{b\,(A)}$
		Fast	9.41±0.28$^{b\,(A)}$	42.42±0.61$^{a\,(A)}$
	P. dissecta	Slow	8.05±0.20$^{a\,(A)}$	45.91±1.19$^{b\,(A)}$
		Fast	8.92±0.19$^{b\,(A)}$	41.36±0.78$^{a\,(A)}$
L. erysimi	*C. sexmaculata*	Slow	9.97±0.29$^{a\,(B)}$	55.82±0.56$^{b\,(B)}$
		Fast	12.76±0.20$^{b\,(B)}$	52.22±0.87$^{a\,(B)}$
	P. dissecta	Slow	10.48±0.26$^{a\,(B)}$	54.32±0.47$^{b\,(B)}$
		Fast	11.12±0.21$^{b\,(B)}$	50.72±1.11$^{a\,(B)}$
R. maidis	*C. sexmaculata*	Slow	10.22±0.56$^{a\,(BC)}$	61.25±0.77$^{b\,(C)}$
		Fast	13.13±0.38$^{b\,(B)}$	58.92±0.71$^{a\,(C)}$
	P. dissecta	Slow	11.63±0.33$^{a\,(C)}$	57.82±1.19$^{b\,(C)}$
		Fast	12.34±0.22$^{b\,(C)}$	53.42±0.68$^{a\,(C)}$
	F$_{\text{Prey species}}$ (P-value); df		60.88 (0.001); 4, 780	41.27 (0.001); 4, 780
	F$_{\text{Ladybird species}}$ (P-value); df		343.31 (0.001); 1, 780	4.85 (0.028); 1, 780
	F$_{\text{Developmental types}}$ (P-value); df		13.11 (0.001); 1, 780	7.11 (0.008); 1, 780
	F$_{\text{Prey species x Ladybird species}}$ (P-value); df		7.10 (0.001); 4, 780	25.99 (0.001); 4, 780
	F$_{\text{Prey species x Developmental types}}$ (P-value); df		9.87 (0.001); 4, 780	16.03 (0.001); 4, 780
	F$_{\text{Ladybird species x Developmental types}}$ (P-value); df		34.60 (0.001); 1, 780	41.76 (0.001); 1, 780
	F$_{\text{Prey species x Ladybird species x Developmental types}}$ (P-value); df		67.12 (0.001); 4, 780	29.35 (0.001); 4, 780

Values are Mean±SE.

For both ladybird species, lower cases represent comparison of means between slow and fast development within ladybird species on each prey species, and upper cases in parentheses represent comparison of means between slow and fast development within ladybird species on different prey species.

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

When the degree of freedom=1, a Yates correction for continuity was employed, while for multiple comparisons, *i.e.* when the degrees of freedom >1, Bonferroni corrections were made using R software (version 3.0.1; R Development Core Team 2013). The data were subjected to a General Linear Model (GLM), using ladybird species, prey species and developmental type (slow/fast) as independent factors and developmental duration, mass of adults and adult longevity as the dependent factors. Treatment means were further tested using Tukey's post hoc honest significance test.

The data on fecundity and percent egg viability taken as dependent factors were checked for normal distribution before subjecting them to a GLM, using prey species, 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 Chi-square tests, were performed using MINITAB 15.0. Percent data were arcsine transformed before GLM followed by a comparison of means using Tukey's post hoc honest significance test.

RESULTS

Immature survival of *C. sexmaculata* (χ^2=57.014; P<0.05; df = 4) and *P. dissecta* (χ^2=68.577; P<0.05; df = 4) differed significantly with the prey species, with maximum survival on *A. craccivora* and *A. gossypii* (Fig. 2). However, the difference in immature survival between ladybird species on each prey was not significant (Fig. 2).

The proportion of slow to fast emergence varied significantly among prey species when beetles were fed on *A. craccivora*, *A. gossypii*, *A. nerii*, *L. erysimi*, and *R. maidis* (Fig. 3). When comparing slow developers across different prey species, significant differences were observed for *C. sexmaculata* (χ^2=40.913; P<0.05; df=4) and *P. dissecta* (χ^2=37.847; P<0.05; df=4). Similar significant differences were noted for fast developers in both species. However, the number of slow developers did not differ significantly between the two ladybird species for any of the prey species: *A. craccivora* (χ^2=0.090; P>0.05; df=1), *A. gossypii* (χ^2=0.655; P>0.05; df=1), *A. nerii* (χ^2=0.022; P>0.05; df=1), *L. erysimi* (χ^2=0.085; P>0.05; df=1), and *R. maidis* (χ^2=0.021; P>0.05; df=1). The highest number of slow developers in both ladybird species was recorded on *A. nerii*, while the lowest was on *A. craccivora* (Fig. 3).

The proportion of males and females among slow and fast developers differed significantly for each prey species (Fig. 4a,b). The proportion of males was higher in fast developers of both species on *A. nerii*, *L. erysimi*, and *R. maidis* (Fig. 4a). Conversely, the proportion of females was higher in slow developers of both ladybird species across all prey species, and also in fast developers of both species on *A. craccivora* and *A. gossypii* (Fig. 4b).

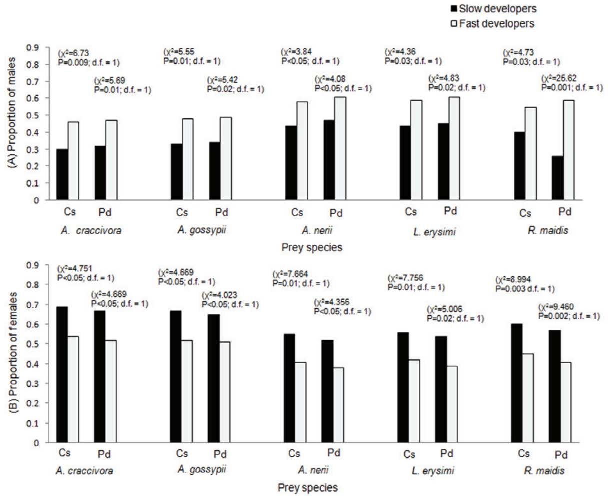

Fig. 4: Graphs depicting proportion of (A) males and (B) females of *Cheilomenes sexmaculata* (Cs) and *Propylea dissecta* (Pd) under slow/fast development on different prey species. Chi-square values (significant at P<0.05) present above each set of bars indicate difference between slow and fast developers of each ladybird species on each prey species.

Total developmental duration of slow and fast developers varied significantly between and within prey species (Fig. 5). GLM revealed that all three independent factors, *i.e.* prey species (F=58.33, P<0.05, df=4, 780), ladybird species (F=61.41, P<0.05, df=1, 780) and developmental types (F=12.52, P<0.05, df=1, 780) had a significant influence on the total developmental duration. The interactions between prey species and developmental types ($F_{interaction}$= 72.58, P=0.001, df=4, 780), ladybird species and developmental types ($F_{interaction}$= 6.13, P=0.013, df=1, 780) and prey species and ladybird species and developmental types ($F_{interaction}$= 3.79, P=0.005, df=4, 780) were significant except for the interaction between prey species and ladybird species ($F_{interaction}$= 1.76, P=0.136, df=4, 780). The longest developmental duration was recorded on *A. nerii* for both slow and fast developers of both the ladybird species.

Fecundity and egg viability of slow and fast developers varied significantly between and within prey species treatments (Table 3). GLM revealed that significantly higher numbers of eggs were laid by fast developers and with a higher percent egg viability than by slow developers. This trend was similar in both species (Table 2).

Body mass and adult longevity of slow and fast developers varied significantly between and within prey species. Adults of fast developers were heavier on all prey species than slow developers, while slow developing adults had higher longevities than the fast developers (Table 2). This trend was similar in both species. These

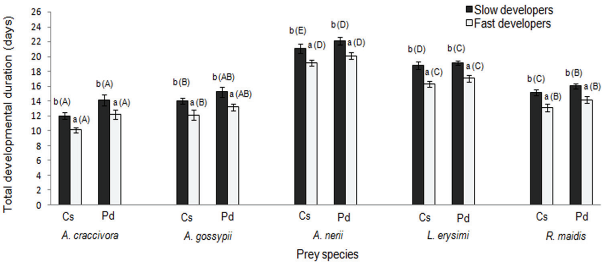

Fig. 5: Total developmental duration of *Cheilomenes sexmaculata* (Cs) and *Propylea dissecta* (Pd) on different prey species. Values are Mean±SE. For both ladybird species, lower cases represent comparison of means between slow and fast development within ladybird species on each prey species, and upper cases in parentheses represent comparison of means between slow and fast development within ladybird species on different prey species. Values followed by different alphabets show significant differences (P<0.05) amongst means of a slow and fast development.

results were also supported by GLM, which revealed that prey species, ladybird species, developmental types and their interactions had a significant influence on body mass and adult longevity (Table 3).

DISCUSSION

In this study, we confirmed the presence of a bimodal distribution pattern with significantly different developmental times within cohorts of *C. sexmaculata* and *P. dissecta*, consistent with the findings of Mishra & Omkar (2012). Our results thus support the hypothesis that the ratio of slow to fast developers varies significantly among different prey species. Both development types took the longest to develop on *A. nerii*, followed by *L. erysimi*, *R. madis*, *A. gossypii* and shortest on *A. craccivora*. Fastest development, higher survival and fecundity of both slow and fast developers on *A. craccivora* and *A. gossypii* reveal them to be the best suited prey species for the development of these two ladybirds.

Co-existence of the two developmental rates within the cohort was observed in insects (Gouws *et al*., 2011), chrysomelid *Z. bicolorata* (Pandey *et al*., 2013) and ladybirds (Mishra & Omkar, 2012; Singh *et al*., 2014). This variation in developmental rates may result from (a) mothers laying eggs with different metabolic rates due to variations in developmental alleles (Sloggett & Lorenz, 2008; Osawa & Ohashi, 2008) or (b) due to differences in egg sizes and nutrient content (Hodek *et al*., 2012). High metabolic rates have been reported to be associated with short developmental periods and high fertility (Marinkovic *et al*., 1986; Hoffmann & Parsons, 1989), while low metabolic rates increase lifespan and stress resistance (Service, 1987; Hoffmann & Parsons, 1989). Egg size is also known to influence insect developmental success, developmental rate, offspring size, and offspring fertility (Tauber *et al*., 1991; Fox & Czesak, 2000). Fast development is frequently linked to enhanced fitness because it is associated with lower larval mortality rates (Benrey & Denno, 1997). This advantage arises because organisms that develop quickly tend to reach a larger size at an earlier stage. Larger size generally reduces vulnerability to predation, a concept known as size-dependent selection or the "bigger is better" hypothesis (Miller *et al*., 1988; Bailey & Howd, 1989). Consequently, individuals that grow rapidly are better equipped to evade predators, giving them a significant survival advantage.

Fast development may also reduce cannibalism, especially in species with male killers (Majerus, 1994). However, rapid growth leads to larger individuals who are more costly to maintain. These larger individuals require more energy and are more susceptible to malnutrition and reproductive dysfunction during times of negative energy balance. (Kuzawa, 2005). Slow-growing individuals have proven to be superior when food resources are scarce and competition is weak (Sevenster & Van Alphen, 1993). It acts as a balancing force to keep the slow developers in the population. By ensuring both developmental types in cohorts, females are more likely to ensure the survival of some of their offspring and thereby improve their fitness, leading to the bet-hedging hypothesis (Hanski, 1988; Hanski & Stahls, 1990; Thomas *et al*., 1998).

The distinction between slow and fast emergence was particularly evident with changes in prey species. Prey nutritional value is a crucial factor, as it significantly influences the developmental and reproductive characteristics of predators (Dixon, 2000; Arijs & De Clercq, 2004; Williams & Flaxman, 2012). The suitability of prey depends on how it is assimilated and utilized after consumption (Vivan *et al*., 2003; Pappas *et al*., 2007). Optimal prey promotes faster growth, reduces larval mortality (Chen *et al*., 2012), and results in larger adults (Michaud, 2005). Therefore, the number of fast developers was higher on *A. craccivora* and *A. gossypii* compared to the other prey, as these species allowed faster developers to grow more effectively and efficiently. In contrast, *A. nerii*, *L. erysimi*, and *R. maidis* are known to be suboptimal prey, containing poor nutritional value and toxic allelochemicals (Omkar & Bind, 2004; Omkar *et al*., 2010). Such suboptimal prey creates a strained vegetative state that is unsuitable for rapid development, increases mortality, and results in skewed ratios favouring slow development under unfavourable conditions. It is believed that differences in the ratios of fast developers indicate increased mortality for certain evolutionary forms; however, this hypothesis requires rigorous experimentation.

The large number of slow-growing females observed in this study may be a result of increased mortality among males, which tend to develop faster. More females were also found in the four species belonging to the tribe Chirocolini and one species belonging to the tribe Cochinellini. This was attributed to certain genetic factors that proved fatal to the males when exposed to stressors (Henderson & Albrecht, 1998). Instead, it is believed that certain male killers are responsible for the high mortality of male ladybird embryos, leading to increased numbers of female ladybirds (Majerus, 2006). Again, conclusive evidence is probably only possible with molecular studies.

In the *C. sexmaculata* and *P. dissecta* cohorts, we found that fast developers were larger than slow developers and had higher female fertility. This is because slow-growing individuals also appear to feed slowly as if they were naturally slow-growing (Dixon, 2000). Variation in fertility was corroborated by differences in body weight (Darwin, 1874) and the number of ovaries that can vary in response to larval feeding (Rhamhalinghan, 1985; Dixon & Guo, 1993). Larger females produce more and larger eggs, which are thought to promote faster development (Stearns, 1992; Cloutier *et al*., 2000; Garcia-Barros, 2000; Katvala & Kaitala, 2001; Roff , 2002; Omkar & Afaq, 2013). Faster growth resulted in earlier maturation, larger adult size, and improved ability to produce large, resilient offspring in the future (Kuzawa, 2005). The present study is consistent with the results of Skorping (2007) who selected fast and slow maturing nematodes and found that fast strains had higher fertility but lower viability than slow strains. The model proposed by Bueno & Lopez-Urutia (2012) also predicted shorter developmental periods for organisms that produce more offspring. Also, the high fertility of rapidly developing females suggests that there may be a trade-off between survival and reproduction (Promislow & Bugbee, 2000; Maklakov *et al*., 2009; Scannapieco *et al*., 2009; Lazarevic *et al*., 2012). Slow-growing individuals conserve more of their resources and nutrients for the maintenance of their somatic cells, resulting in lower energy availability, slower growth, delayed sexual maturity, and lower production of gonadal steroids, it has been suggested to cause short adult stature and reduced fertility (Arendt, 1997; Kuzawa , 2005, 2008; Walker *et al*., 2006).

The percent egg viability was also higher in the fast developers. Larger size is associated with better genetic signatures (Helinski & Harrington, 2011). Lewis *et al*. (2010) found that males from slower-evolving strains produced fast developing *Drosophila* homozygous strains had higher egg viability (Partridge & Fowler, 1992). Roper *et al*. (1993) and Chippindale *et al*. (1994) showed that slow-growing flies suffer from inbreeding suppression.

Current study reveals that both ladybird species exhibit the presence of slow and fast developers across all prey species. Additionally, the ratio of slow to fast developers varies with different prey species, showing similar trends in both ladybird species. The highest number of fast developers was recorded on *A. craccivora*, which is likely the most nutritious aphid species, while the lowest number was found on *A. nerii*, probably the least nutritious. Slow developers consistently showed a female-biased sex ratio and longer lifespans across all prey species. Furthermore, fast developers were consistently heavier than slow developers, regardless of the prey or ladybird species. Fast developers fed on *A. craccivora* and *A. gossypii* laid more eggs with higher viability. Overall, the results indicate the coexistence and stability of slow and fast development within an egg batch. The apparent constancy of the ratio at oviposition suggests that it is a genetic trait conserved across ladybird species, which could be utilized to enhance fast developers through selection across generations. Such purified lines could be targeted for use in biological control applications.

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