Allocation of food resource by experimentally evolved lines of developmental variants of *Propylea dissecta*: a food exploitation strategy

Arshi Siddiqui[1,2] (iD), Omkar[1] and Geetanjali Mishra[1]

[1]Ladybird Research Laboratory, Department of Zoology, University of Lucknow, Lucknow, Uttar Pradesh 226007, India and [2]Department of Bioscience, Integral University, Dasauli Kursi road, Lucknow, Uttar Pradesh 226026, India

Abstract

The effects of selection on developmental variants have not yet been rigorously investigated on variable prey quantities. We investigated the food exploitation strategy of first (F_1) and fifteenth (F_{15}) generation slow and fast developers of *Propylea dissecta* (Mulsant) in the presence of scarce and abundant quantities of pea aphid, *Acyrthosiphon pisum* (Harris), and its effect on adult body mass and reproductive attributes. Both selected slow developers and selected fast developers were higher in number than their counter unselected generation on scarce and abundant diets, respectively. Immature survivals of selected slow developers were depressed after the selection process while it was enhanced for selected fast developers on both diet regimes. On both diets, the total developmental duration was longer for selected slow developers and shorter for selected fast developers. Fecundity and percent egg viability were greater in selected fast developers with plentiful prey supply and lower in control slow developers with inadequate prey supply. More adult body mass was found for pre-selected slow developers than selected slow developers on a scarce diet but selected fast developers enhanced their body weight than unselected individuals of fast developers on an abundant diet. The present experimental evolution findings point to the presence and persistence of developmental variations with variability in their developmental and reproductive traits on allocating scarce and abundant prey supplies.

Introduction

Intraspecific variation occurs when a species' anatomy, physiology, behavior, and social organization change as it adjusts to changing environmental conditions by modifying its dietary behaviors (Wcislo, 1989). Such variation may be directly related to genetic differences between individuals within a species (Honěk, 1993). The development of individuals within a population plays an important role in regulating the population (Sih *et al.*, 2012). But regardless of the suitable abiotic and biotic conditions, variations in the development rate have been found in many insect predators (Pandey *et al.*, 2013). This variation in development rate within an egg batch is termed developmental rate polymorphism (DRP) and has been a source of fascination for researchers. The existence of DRP under optimal conditions in an aphidophagous ladybirds, *Menochilus sexmaculatus* (Fabricius) (Singh *et al.*, 2016) and *Propylea dissecta* (Mulsant) (Siddiqui *et al.*, 2017) and Parthenium beetle, *Zygogramma bicolorata* (Pallister) (Pandey *et al.*, 2013; Afaq *et al.*, 2021) reveals its genetic regulation under the influence of abiotic factors on developmental variants but biotic factors are still unexplored, especially to relative prey abundance on selected lines. The differential developmental rates under differing conditions exist commonly but the existence of two rates of development in a cohort under each environmental condition is still a mystery. This is possibly a way for a particular species to escape from unfavorable environmental conditions, or it could be the emerging individual's genetic or predetermined perspective. Studies have also revealed that such populations are examined across a number of generations under defined conditions that may be repeated, whether in a laboratory settings or in the nature (Rajpurohit *et al.*, 2016; Bono *et al.*, 2017).

In ladybirds, developmental variants (slow and fast developers) are found in each cohort (Singh *et al.*, 2016), and are governed by genetic factors (Bailey and Bataillon, 2016). The development is species-specific and strongly dependent on the ambient temperature (Afaq *et al.*, 2021), photoperiod (Bono *et al.*, 2017), population density (Ungerová *et al.*, 2010), and quality and quantity of food (Singh *et al.*, 2016). However, the ability of a predator to survive, develop, and reproduce in prey-scarce conditions is the most important aspect that determines the fitness of their own immature stages during development (Singh *et al.*, 2016) and its biocontrol potential (Siddiqui *et al.*, 2015, 2017). The prey consumption seemingly decreases with the increase in developmental duration (Siddiqui *et al.*, 2017; Pervez and Sharma, 2021). The fast-growing individuals are more vulnerable to starvation owing to their need to sustain

higher metabolic rates (Sundström and Devlin, 2011). The optimal growth rate is often lower than the maximum rate achievable indicating that rapid growth is costly (Metcalfe and Monaghan, 2001). Also, rapid growth may be associated with reduced developmental control and an increased developmental error (Nylin and Gottard, 1998).

If the costs of maintaining conversions are significant (Edelaar et al., 2005), selection will quickly remove it from an environment with a little relevance, however, there are substantial demands on resource allocation other than maintaining plasticity levels. In spite of having been so many works on ladybirds, the effect of abiotic and biotic factors on selection is still unexplored. Therefore, the present study was conducted to evaluate the food allocation strategy on scarce and abundant prey supplies among the intraspecific control (pre-selected/F_1) and (post-selected/F_{15}) selected individuals of P. dissecta whether the control variants (slow/fast) exploit more food than that of post-selected one or their consumption remains constant after a selection process. The results will help understand the strategies of control and selected slow and fast developers and helping in the mass multiplication of predatory ladybirds for their use in biocontrol of various pest species.

Material and methods

Stock maintenance

The wild P. dissecta population was taken from agricultural regions near Lucknow, Uttar Pradesh, India (16.8470°N, 80.9470°E) to be used as laboratory stock. Under standard laboratory settings [27 ± 1°C temperature; 65 ± 5% relative humidity and 14L:10D photoperiod in a BOD Incubator (YORCO; York Scientific Industries Pvt. Ltd., India)], they were raised in clear plastic Petri dishes (9.0 × 2.0 cm) and fed ad libitum pea aphid Acyrthosiphon pisum (Harris) (Hemiptera: Aphididae) (reared under standard greenhouse condition on their mentioned host plant) bred on the broad bean. After an initial mass collection, the stock was continually replenished with wild captured individuals throughout the season to minimize inbreeding. In the BOD incubator, mature males and females were coupled in Petri dishes (size and conditions as above). The females mated and laid eggs, which were separated every 24 h and the prey were replenished. Under aforementioned lab conditions, the newly hatched larvae were individually reared for further experimental setups.

Separation of lines of slow and fast developers

Into individual Petri dishes (size as above) 100 virgin males and females, each were taken from the outbred laboratory stock, were placed along with ad libitum of A. pisum. To prevent egg cannibalism, a single batch of eggs was gathered from each mate. They were observed every 12 h for hatchings. The newly hatched first instars were separated and reared individually till adults emerged (under the aforesaid laboratory settings). Based on their total developmental duration (from egg to adult), the emerging adults were divided into two categories: slow developers and fast developers. Furthermore, 'slow developers' have long total developmental periods and 'fast developers' have a short developmental period. Using a random breeding method to minimize pairing between siblings or close relatives, two distinct developmental lines were formed by mating slow–slow developers and fast–fast developers for up to ten generations (Swallow and

Garland, 2005). Following that, mixed matings were performed among individuals of either developmental variation to minimize inbreeding depression (slow or fast developers; Swallow and Garland, 2005), for an additional five generations. Newly emerged from slow and fast developing adults in the F_{15} generation (experimental generation) and the F_1 generation (control) were then used to evaluate the following mentioned parameters. After 6 h, the weight of the newly emerged adults was recorded. The percent of immature survival (number of surviving out of a total number of eggs), slow–fast emergence ratio (number of slow or fast developers/total number of individuals emerged), and fecundity with percent egg viability (10 days old) were calculated in F_1 and F_{15} generation of both slow and fast developers.

Experimental design

For the study, we followed the standardized prey quantity and experimental regime for prey-scarce and prey-abundant conditions for P. dissecta by Singh et al. (2016). Ten-day-old unmated adults (ten pairs) from each of F_1 (control) and F_{15} (selected) generation of each developmental variant were paired in separate plastic Petri dishes (9.0 × 2.0 cm) and placed on different prey quantities, viz. prey-scarce (3–5 second and third instars of A. pisum per day) and prey-abundant (25–30 second and third instars of A. pisum per day) conditions. A total of 250 eggs from the first 5 days of oviposition of both generations (F_1 and F_{15}) of each developmental variant on each prey quantity were selected. Hatched instars were individually reared in Petri dishes (9.0 × 2.0 cm) on the same prey quantity as provided to their parents till adult emergence. They were observed twice a day for survival and molting. After 6 h, the weight of the newly emerged adults weighed using electronic balance (Sartorius CP225-D; 0.01 mg precision) was recorded. The percent of immature survival (number of surviving out of a total number of eggs) and slow-fast emergence ratio was calculated for both F_1 and F_{15} generations of each variant. The newly emerged adults (10 days old) of each type, i.e. slow and fast developers, were paired in Petri dishes (size as above) and provided with the same prey supply on which they had completed development. Daily oviposition was recorded for the next 20 days and egg viability was recorded in mating pairs from each type (i.e. slow and fast) for both control and selected lines, respectively.

Statistical analysis

To check for normal distribution, data on total developmental periods of variations (egg to adult) were subjected to the Kolmogorov–Smirnov test of normality. The total developmental duration of slow and fast developers of P. dissecta of F_1 and F_{15} generation when fed on scarce and abundant prey quantity was not normally distributed (table 1). The frequency data of the developmental durations were then graphed to show distribution patterns, which was found to be bimodal (fig. 1).

All percent data were subjected to arcsine square root transformation before further analysis. General linear MANOVA was conducted with generation (F_1 and F_{15}), prey quantity (abundant and scarce), developmental variant (slow/fast), acting as independent factors and developmental duration, adults body mass as a dependent factor. The χ^2 'goodness of fit' analysis was used for the comparison of emergence ratio of slow and fast developers, survival for both control, and selected line of slow and fast developers. Means were compared using post hoc Tukey's honest

Table 1. Normality of developmental duration of variants of *P. dissecta* on scarce and abundant prey supply

Prey quantity	Developmental variants	Generations	Normality of data
Scarce	Slow developers	Control (F_1)	$D+$: 0.026 $D-$: 0.034 D: 0.0034; P-value > 0.05
		Selected line (F_{15})	$D+$: 0.040 $D-$: 0.050 D: 0.050; P-value > 0.05
	Fast developers	Control (F_1)	$D+$: 0.037 $D-$: 0.036 D: 0.037; P-value > 0.05
		Selected line (F_{15})	$D+$: 0.047 $D-$: 0.051 D: 0.051; P-value >0.05
Abundant	Slow developers	Control (F_1)	$D+$: 0.074 $D-$: 0.080 D: 0.080; P-value > 0.05
		Selected line (F_{15})	$D+$: 0.041 $D-$: 0.034 D: 0.041; P-value > 0.05
	Fast developers	Control (F_1)	$D+$: 0.056 $D-$: 0.045 D: 0.056; P-value > 0.05
		Selected line (F_{15})	$D+$: 0.051; $D-$: 0.069 D: 0.069; P-value > 0.05
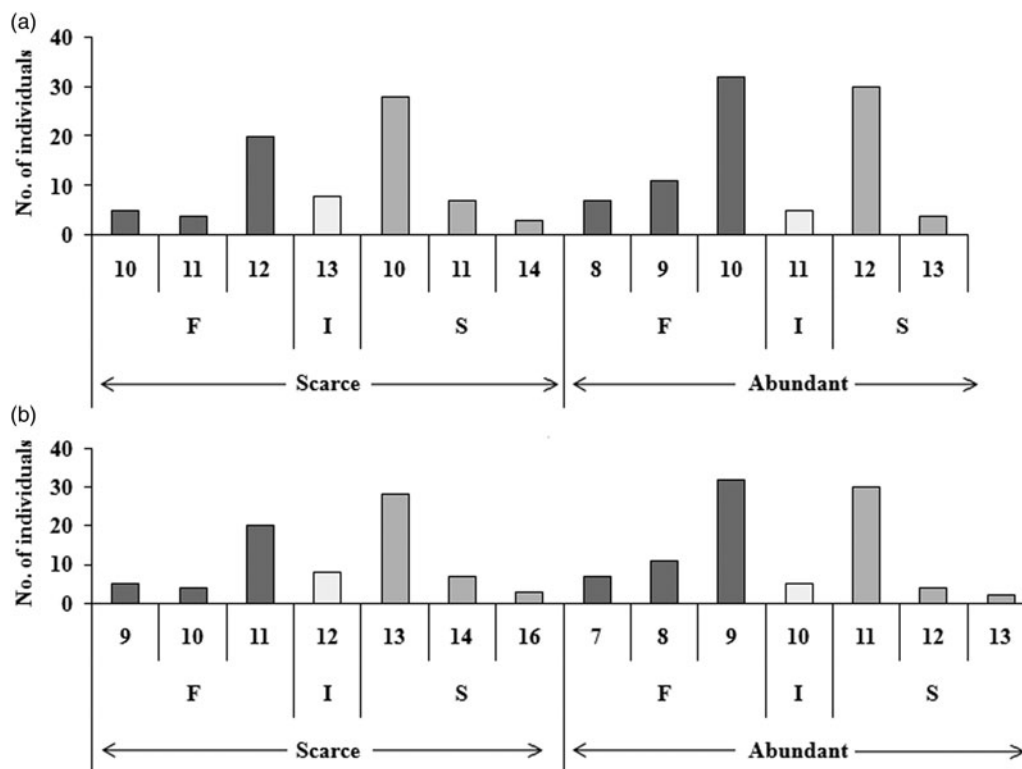
Figure 1. Frequency distribution of total developmental duration (TDD) of (a) control (F_1) and (b) selected line (F_{15}) of slow and fast developers of *P. dissecta* at scarce and abundant prey supply. Bars indicate number of individuals emerging at each developmental duration. '*F*' indicates fast developers while '*I*' and '*S*' indicate intermediate and slow developers, respectively.

significance test at 5% levels. All statistical analyses were performed using MINITAB 15.0. Mortality value or '*k*' value was calculated from life table attributes following Morris and Miller (1954) and Southwood (1978).

Results

The fecundity of selected fast developer females was higher than those of control fast developer females on abundant prey supply. Further analysis showed maximum fecundity by selected fast developers on abundant prey supply and minimum by selected slow developers on scarce prey supply (table 2). The interactions between developmental variants and generation and prey quantity and developmental variants were significant but the interaction

between prey quantity and generation along with the interaction of all three independent factors were insignificant (table 2).

Percent egg viability of control and selected developmental variants was higher in selected fast developers on abundant prey supply and lower in control slow developers on scarce prey supply. The MANOVA results also revealed a significant influence of prey quantity generation, and developmental variants on percent egg viability while the interactions between developmental variants and generation and prey quantity and developmental variants were significant but the interaction between prey quantity and generation along with the interaction of all three independent factors were insignificant (table 2).

The maximum selected slow developers were recorded when the larvae were fed on scarce and minimum in slow developers

Table 2. Reproductive attributes of developmental variants of control and selected line of *P. dissecta* on scarce and abundant prey supply

Prey quantity	Developmental variants	Generations	Fecundity (no. of eggs)	Egg viability (%)
Scarce	Slow developers	Control (F_1)	146.10 ± 4.78^{bA}	30.93 ± 2.75^{aA}
		Selected line (F_{15})	130.27 ± 11.18^{aA}	35.72 ± 1.75^{bA}
	Fast developers	Control (F_1)	200.20 ± 37.82^{aB}	34.15 ± 7.10^{aB}
		Selected line (F_{15})	236.30 ± 34.15^{bB}	45.90 ± 2.56^{bB}
Abundant	Slow developers	Control (F_1)	338.65 ± 11.18^{bA}	63.63 ± 2.28^{aA}
		Selected line (F_{15})	228.10 ± 21.20^{aA}	68.30 ± 3.99^{bA}
	Fast developers	Control (F_1)	740.50 ± 36.26^{aB}	74.79 ± 2.55^{aB}
		Selected line (F_{15})	850.97 ± 26.45^{bB}	82.61 ± 1.72^{bB}
$F_{Prey\ quantity}$ (*P*-value); df			$F = 1063.75$ ($P = 0.001$); df = 1, 112	$F = 507.46$ ($P = 0.001$); df = 1112
$F_{Generations}$ (*P*-value); df			$F = 0.69$ ($P > 0.05$); df = 1, 112	$F = 7.17$ ($P = 0.009$); df = 1, 112
$F_{Developmental\ variants}$ (*P*-value); df			$F = 376.77$ ($P = 0.001$); df = 1, 112	$F = 48.60$ ($P = 0.001$); df = 1, 112
$F_{Prey\ quantity \times Generations}$ (*P*-value); df			$F = 0.33$ ($P > 0.05$); df = 1, 112	$F = 1.14$ ($P > 0.05$); df = 1, 112
$F_{Developmental\ variants \times Generations}$ (*P*-value);df			$F = 21.62$ ($P = 0.001$); df = 1, 112	$F = 6.82$ ($P = 0.010$); df = 1, 112
$F_{Prey\ quantity \times Developmental\ variants}$ (*P*-value); df			$F = 199.30$ ($P = 0.001$); df = 1, 112	$F = 5.49$ ($P = 0.021$); df = 1, 112
$F_{Generations \times Developmental\ variants \times Prey\ quantity}$ (*P*-value); df			$F = 2.96$ ($P > 0.05$); df = 1, 112	$F = 0.34$ ($P > 0.05$); df = 1, 112

Values are mean ± SE.
Small letters represent comparison of means between slow–slow and fast–fast developers of both generations on each prey species.
Capital letters represent comparison of means between slow and fast developers of control and selected line within a prey species.

from control on abundant prey supply. Further, maximum selected fast developers were recorded on abundant diet and minimum unselected fast developers on scarce prey (fig. 2).

The percent immature survival was highest in selected fast developers than unselected fast developers on both prey supplies while the immature survival was suppressed after selection in slow developers. The data revealed maximum immature survival of selected fast developers on abundant while minimum by control fast developers on scarce prey supply (fig. 3). The χ^2 revealed a significant difference between slow/fast developers of both control and selected line on scarce and abundant diets, respectively.

Tukey's post hoc comparison of individual means showed a statistically significant difference between the total developmental duration of control and selected developmental variants. The longest duration was of selected slow developers on a scarce diet while shortest was of selected fast developers on an abundant diet. General linear MANOVA revealed a statistically significant effect of prey quantity, generations (F_1 and F_{15}), and developmental variants (slow and fast developers) on the total developmental duration (days). Interactions between prey quantity and generation, developmental variants and generations, prey quantity and developmental variants all three independent factors were significant (table 3).

The fast developers showed the heaviest adult body mass when fed on abundant diet and lowest by slow developers on scarce diet irrespective of generation (table 3). Comparison of means revealed that selected fast developers were heavier than other developmental variants of both F_1 and F_{15} generations. The interactions between prey quantity and generation; developmental variants and generations; prey quantity and developmental variants; amid interactions between all three independent factors were significant (table 3).

Comparison of kappa (k) value revealed the highest value for F_1 on scarce diet (0.200) > F_1 on abundant diet > F_{15} on scarce diet > F_{15} on abundant diet (fig. 4). However, the mortality values

or 'k' values were lowest for the selected individuals on abundant diet and highest for control individuals on a scarce diet.

Discussion

The results revealed significant differences between the control individuals of *P. dissecta* than those selected after 15 generations. The results indicate the presence of developmental variants in F_1 and F_{15} generation on a scarce and abundant diet. Prey quantity significantly influenced the developmental duration, reproduction, and mortality value of both generations' developmental variants.

Divergence in a number of emerged individuals was significant but not in the emergence ratio, indicating major differences in control and selected variants. During the development of *P. dissecta*, some larvae develop fast and some develop slowly. A high metabolic rate is linked with a short developmental period and high fecundity (Hoffmann and Parsons, 1989). The study reveals that minimum biomass is required to completely develop earlier than slow developers (Huges, 1980).

From the ecological point of view, the reason for fast emergence might be to minimize local extinction by catastrophic events (Thomas *et al.*, 1998). On a physiological basis this might be due to hatching asynchronization (Osawa, 1992), eggs with different metabolic rates due to allelic differences (Sloggett and Lorenz, 2008), and/or mother laying eggs with different sizes and nutritional content (Hodek *et al.*, 2012). Thus, seemingly some unknown mechanisms operate during the development of *P. dissecta* that enhance or inhibit the pace of development so it continues throughout the generational rearing. This shows that an egg batch of *P. dissecta* possesses selectable genetic variation for the developmental duration. This might be the product of differential environmental induction of genomic programs that guide trade-offs allocated toward different traits
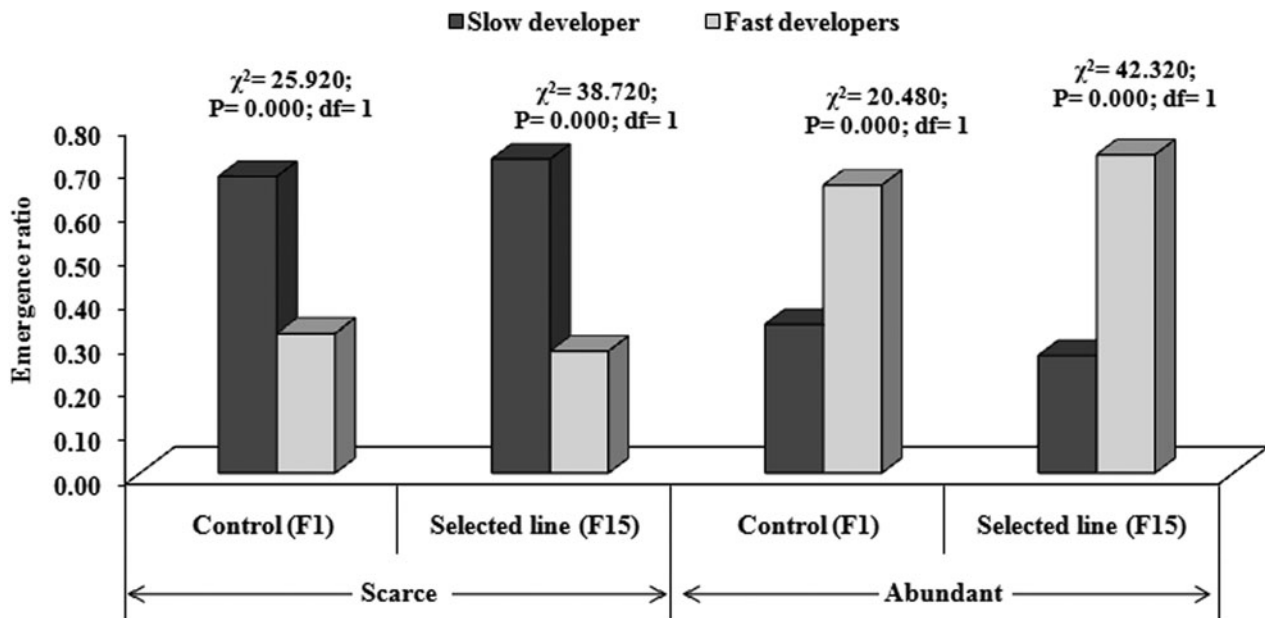
Figure 2. Effect of scarce and abundant prey supply on slow:fast emergence ratio of control (F_1) and selected line (F_{15}) of *P. dissecta*.
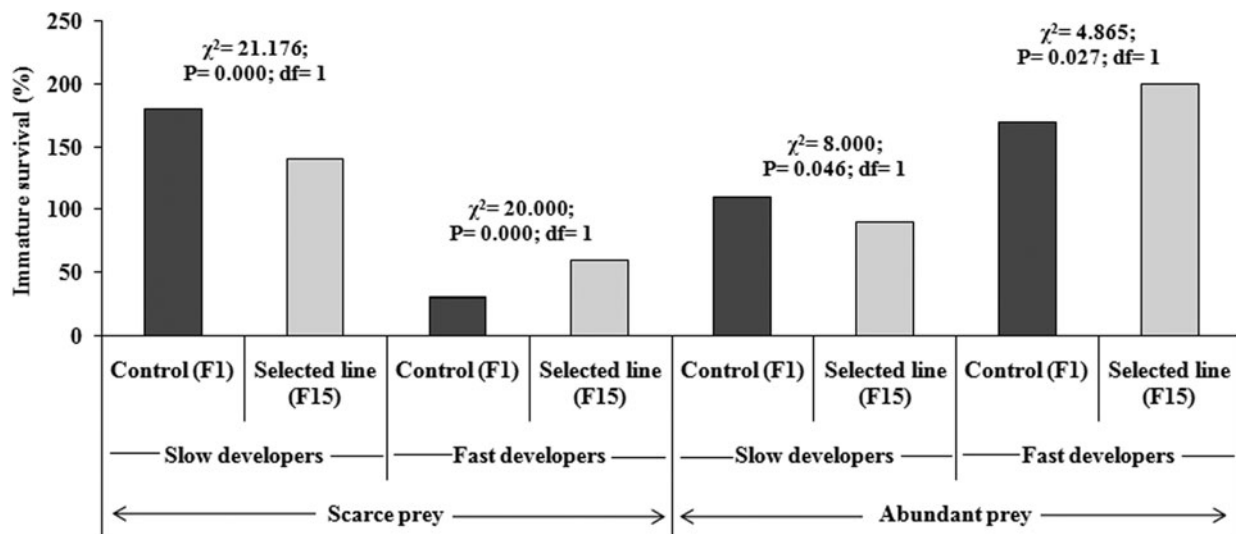

Figure 3. Effect of scarce and abundant prey supply on immature survival of control (F_1) and selected line (F_{15}) of slow and fast developers of *P. dissecta*.

during development in response to intrinsic and extrinsic cues (Snell, 2013).

Previous studies in other insects like bean weevil, *Acanthoscelides obtectus* (Say) (Darka and Nikola, 2013) and flour beetles, *Tribolium castaneum* Herbst, and *T. confusum* (Giraldeau and Caraco, 2018) also confirm the effect of relative prey abundance on various parameters. Similar findings were also reported in the European cabbage butterfly, *Pieris rapae* (Linnaeus) in which fast-developing larvae were often less parasitized than slow-developing ones, and were no evidence for a positive relationship between development time and the incidence of parasitism (Benrey and Denno, 1997), myrmecophilous butterfly, *Maculinea rebeli* (Hirchke) (Thomas *et al.*, 1998), Indian meal moth, *Plodia interpunctella* (Hubner) (Naeemullah and Takeda,

1998), maturing worms (Skorping, 2007), and ladybirds, *M. sexmaculatus* (Singh *et al.*, 2016) and *P. dissecta*. Thus, the present study revealed a significant effect of prey supply on slow and fast developers in the F_1 and F_{15} generations. Hoffmann and Parsons (1989) reported in *Drosophila melanogaster* Meigen that lines selected for increased resistance to many environmental stresses have lowered metabolic rate and behavioral activity levels.

Previous studies indicated a similar ratio of slow and fast developers in coccinellids, *P. dissecta* and *M. sexmaculatus* (Singh *et al.*, 2016), and Chrysomelidae, *Z. bicolorata* Pallister (Afaq *et al.*, 2021) on standard and variable abiotic conditions. Our study reveals a maximum number of selected slow developers on scarce diets and selected fast developers on abundant diets in both F_1 and F_{15} generations. This shift probably allows individuals

Table 3. Total development duration and body mass of slow and fast developers of control and selected line of *P. dissecta* on scarce and abundant prey supply

Prey quantity	Developmental variants	Generations	Total development duration (days)	Body mass of adults (mg)
Scarce	Slow developers	Control (F_1)	17.18 ± 0.15^{aB}	09.10 ± 0.07^{bA}
		Selected line (F_{15})	20.42 ± 0.16^{bB}	08.05 ± 0.16^{aA}
	Fast developers	Control (F_1)	12.60 ± 0.13^{bA}	10.06 ± 0.29^{aB}
		Selected line (F_{15})	11.24 ± 0.13^{aA}	11.08 ± 0.09^{bB}
Abundant	Slow developers	Control (F_1)	12.00 ± 0.21^{aB}	13.08 ± 0.29^{bA}
		Selected line (F_{15})	13.48 ± 0.15^{bB}	10.73 ± 0.10^{aA}
	Fast developers	Control (F_1)	10.48 ± 0.12^{bA}	14.13 ± 0.11^{aB}
		Selected line (F_{15})	09.34 ± 0.10^{aA}	15.76 ± 0.10^{bB}
$F_{\text{Prey quantity}}$ (P-value); df			$F = 1516.48$ (P-value: 0.001); df = 1, 399	$F = 331.66$ (P-value: 0.001); df = 1, 399
$F_{\text{Generations}}$ (P-value); df			$F = 28.69$ (P-value: 0.001); df = 1, 399	$F = 7.44$ (P-value: 0.007); df = 1, 399
$F_{\text{Developmental variants}}$ (P-value); df			$F = 2195.47$ (P-value: 0.001); df = 1, 399	$F = 143.37$ (P-value: 0.001); df = 1, 399
$F_{\text{Prey quantity} \times \text{Generations}}$ (P-value); df			$F = 13.81$ (P-value: 0.001); df = 1, 399	$F = 227.42$ (P-value: 0.001); df = 1, 399
$F_{\text{Developmental variants} \times \text{Generations}}$ (P-value); df			$F = 303.46$ (P-value: 0.001); df = 1, 399	$F = 105.13$ (P-value: 0.001); df = 1, 399
$F_{\text{Prey quantity} \times \text{Developmental variants}}$ (P-value); df			$F = 381.94$ (P-value: 0.001); df = 1, 399	$F = 30.79$ (P-value: 0.001); df = 1, 399
$F_{\text{Generations} \times \text{Developmental variants} \times \text{Prey quantity}}$ (P-value); df			$F = 22.82$ (P-value: 0.001); df = 1, 399	$F = 175.23$ (P-value: 0.001); df = 1, 399

General linear MANOVA shows effect of prey quantity, generation and developmental variants and their interactions on these parameters.
Values are mean ± SE.
Small letters represent comparison of means between slow–slow and fast-fast developers of both generations on each prey species.
Capital letters represent comparison of means between slow and fast developers of control and selected line within a prey species.
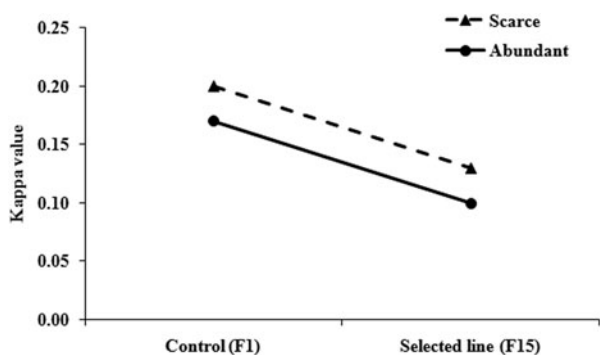
Figure 4. Kappa value of immature stages of control (F_1) and selected lines (F_{15}) of *P. dissecta* on scarce and abundant prey supply.

to maximize fitness by allocating resources differentially among phenotypic traits (Kasumovic and Hall, 2011). The variation in the number of slow and fast developers within diets possibly indicates the increased mortality of a particular development stage on each diet but the ratio remains constant in F_1 and F_{15} generation, which might be a kind of individual strategy of resource allocation in accord to the recent situation. This may probably be due to the increased efficiency of slow developers in attaining the minimum weight required for successful completion of development than fast developers (Huges, 1980). The reduced efficiency of selected slow developers might be due to attaining the threshold weight for achieving the next developmental stage and/or the higher sensitivity to starvation, which may result in their higher mortality (Rotkopf *et al.*, 2013) and low body mass in a selected line. Previous studies also showed increased conversion efficiencies at low levels of food consumption were also reported in aphidophagous mirids and chrysopids (Zheng *et al.*, 1993).

A strong positive correlation between fecundity and egg viability in both abundant and scarce prey conditions was recorded in this study, i.e. when prey quantity was reduced, and then the fecundity and percent egg viability were also reduced. This negative influence of reduced prey quantity can be attributed to the availability of decreased nutrient resources, which restrict the development and reproduction of the predator (O'Brien *et al.*, 2005). Overall fecundity of developmental variants of F_1 and F_{15} generation was low under scarce prey supply, which can be imputed to reduced nutrient resources hindering the development as well as the reproduction of the ladybirds (Majerus, 1994; Moczek, 1998) but as a generational effect, this was minimum in selected slow developers and unselected fast developers. This might be due to the gradual slow process of ovariole development (Evans, 2003) and resorption of eggs (Cope and Fox, 2003) in selected slow developers or might be due to low consumption rate than that of fast developers. Besides, Reznik and Vaghina (2013) reported that nutrients (quality and quantity of prey) affect the rate of reproductive maturation and fecundity in *Harmonia axyridis* Pallas. Maximum fecundity in selected fast developers might be due to improved strain due to the selection process. Since food quantity greatly influences the intrinsic growth and reproductive rates of ladybirds (Lawo and Lawo, 2011), selected individual of fast developers of *P. dissecta* showed the highest oviposition and egg viability under abundant prey conditions. Thus, it may be inferred that the life history traits change in response to nutrient stress. However, the successful development of both larvae and adults under food-stressed conditions suggest the occurrence of strong selection pressure in the natural population of ladybird beetle for survival and reproduction even under adverse conditions.

The higher egg viability by selected fast developers may be due to the large size of males (unpublished data) that possibly supply higher ejaculate, the better quality of genes in addition to accessory gland proteins (Helinski and Harrington, 2011).

This might be due to the effect of continuous rearing of identical lines. Lower fecundity in both F_1 and F_{15} generation but enhanced egg viability in selected slow developers might be due to accelerated fitness shift for healthier parts and survivorship of slow developers. Studies also revealed that reduced egg viability under prey-scarce conditions as recorded in the present investigation may be attributed to (i) reduction in sperm or ancillary fluid production, which in turn might limit female reproductive output (Droney, 1996), and (ii) reduced sperm production due to slow spermatogenesis and a lower rate of sperm survival in the males (Ponsonby and Copland, 1998).

According to Schuder *et al.* (2004), slowing down larval development during food-scarce conditions is one of the several mechanisms (like increase in conversion and exploitation efficiencies, etc.) displayed by larvae to compensate for a lack of food. Studies have shown that if food scarcity occurs before attaining the critical weight, several species extend their last larval duration beyond normal lengths (Nijhout *et al.*, 2006). Thus, the longer developmental durations on scarce prey in selected slow developers in the present study may be due to the following reasons: (i) lengthening of developmental duration as a mechanism that allows the individuals to extend their feeding activity and acquire more opportunities to find and consume the necessary amount of prey or non-prey food to easily reach the critical weight (Shafiei *et al.*, 2001) and (ii) if the fluctuation in food quantity occurs after attaining the critical weight, then the insects cease their growth without change in developmental duration and form resting stage, a phenomenon known as 'determinate development' (Nijhout *et al.*, 2006). In the present study adults resulting from a scarce prey had smaller body mass while those fed on abundant diet result in larger adults. It is supported by many workers (Agarwala *et al.*, 2008). But body mass was enhanced in selected fast developers and depressed in selected slow developers which might be due to continuous cross-mating between slow–slow developers which results in low-weight offspring. Thus, more slow developers with a smaller adult's body mass that emerge under prey-scarce conditions probably have a lower reproductive success based on their smaller size, as suggested by many earlier researchers (Omkar and Afaq, 2013).

Minimum mortality on an abundant diet is probably due to availability of enough prey resources to exploit and reach the minimum threshold weight necessary for changing into the next developmental stage. Also, evolutionary theory illustrates that fast development occurs under suitable conditions and slow development occurs under adverse conditions (e.g. Chown and Gaston, 2010). On scare diet, the mortality value of selected individuals was higher than that of selected individuals on abundant diet which was probably due to gradual acclimatization or transfer of unfavorable conditions in terms of food supply from grandparents to their grand progeny through some unknown genetic cues.

Conclusions

The study revealed that slow and fast developers are present at both scarce and abundant diets in F_1 and F_{15} generation with the discrepancy in emerger's number, fecundity, percent egg viability, and mortality. On a scarce diet, selected slow developer promotes the survival of ladybirds. The slow developers were higher in number on a scarce diet in F_{15} generation. However, on the abundant diet, the selected fast developers were higher in number, and developmental duration of immature stages on scare diet was high as compared to abundant diet (personal observation). This

knowledge will help to understand that within an egg batch different rate polymorphisms were also found after being selected for 15 generations on both diets. Our results demonstrate that both the nutrient and selected line of variants affect the expression of the development rate, fecundity, and mortality of selected traits, but more importantly, that the environmental effects interact in complex ways with evolution experiments. Consequently, the food exploitation strategy was modified accordingly to generational rearing and intraspecific allocation for survival. Our study will provide a source of fascination for a number of evolutionary biologists. The selection of slow and fast developers of *P. dissecta* acts as a possible genetic tool for overall quality improvement and survival strategy for their offspring.

References

Afaq U, Kumar G and Omkar (2021) Is developmental rate polymorphism constant? Influence of temperature on the occurrence and constancy of slow and fast development in *Zygogramma bicolorata* Pallister (Coleoptera: Chrysomelidae). *Journal of Thermal Biology* **100**, 103043.

Agarwala BK, Yasuda H and Sato S (2008) Life history response of a predatory ladybird, *Harmonia axyridis* (Coleoptera: Coccinellidae), to food stress. *Applied Entomology and Zoology* **43**, 183–189.

Bailey SF and Bataillon T (2016) Can the experimental evolution programme help us elucidate the genetic basis of adaptation in nature? *Molecular Ecology* **25**, 203–218.

Benrey B and Denno RF (1997) The slow-growth-high-mortality hypothesis: a test using the cabbage butterfly. *Ecology* **78**, 987–999.

Bono LM, Smith Jr. LB, Pfennig DW and Burch CL (2017) The emergence of performance trade-offs during local adaptation: insights from experimental evolution. *Molecular Ecology* **26**, 1720–1733.

Chown SL and Gaston KJ (2010) Body size variation in insects: a macroecological perspective. *Biological Review* **85**, 139–169.

Cope JM and Fox CW (2003) Oviposition decisions in the seed beetle *Callosobruchus maculates* (Coleoptera: Bruchidae): effects of seed size on super parasitism. *Journal of Stored Product Research* **39**, 355–365.

Darka S and Nikola T (2013) Selection for developmental time in bean weevil (*Acanthosceildes obtectus*): correlated responses for other life history traits and genetic architecture of line differentiation. *Entomologia Experperimentalis et Applicata* **106**, 19–35.

Droney DC (1996) Environmental influences on male courtship and implications for female choice in a lekking Hawaiian *Drosophila*. *Animal Behaviour* **51**, 821–830.

Edelaar P, Piersma T and Postma E (2005) Retained non-adaptive plasticity: gene flow or small inherent costs of plasticity? *Evolutionary Ecology Research* **7**, 489–495.

Evans EW (2003) Searching and reproductive behaviour of female aphidophagous ladybirds (Coleoptera: Coccinellidae): a review. *European Journal of Entomology* **100**, 1–10.

Giraldeau LA and Caraco T (2018) *Social Foraging Theory*. Princeton, New Jersey: Princeton University Press.

Helinski MEH and Harrington LC (2011) Male mating history and body size influence female fecundity and longevity of the dengue vector *Aedes aegypti*. *Journal of Medical Entomology* **48**, 202–211.

Hodek I, Van Emden HF and Honek A (2012) *Ecology and Behaviour of the Ladybird Beetles (Coccinellidae)*. Hoboken, New Jersey, UK: A John Wiley and Sons, Ltd., Publication, p. 4229.

Hoffmann A and Parsons PA (1989) An integrated approach to environmental stress tolerance and life-history variation: desiccation tolerance in *Drosophila*. *Biological Journal of Linnean Society* **37**, 117–136.

Honěk A (1993) Intraspecific variation in body size and fecundity in insects: a general relationship. *Oikos* **66**, 483–492.

Huges G (1980) Larval competition in serially transferred populations of *Drosophila melanogaster*. *Oecologia* **45**, 396–403.

Kasumovic MM, Hall MD, Try H and Brooks R (2011) The importance of listening: allocation shifts in response to the juvenile acoustic environment. *Journal of Evolutionary Biology* **24**, 1325–1334.

Lawo JP and Lawo NC (2011) Misconceptions about the comparison of intrinsic rates of natural increase. *Journal of Applied Entomology* **135**, 715–725.

Majerus MEN (1994) *Ladybirds (New Naturalist 81)*. London: Harper-Collins.

Metcalfe NB and Monaghan P (2001) Compensation for a bad start: grow now, pay later? *Trends in Ecology and Evolution* **16**, 254–260.

Moczek AP (1998) Horn polyphenism in the beetle *Onthophagus taurus*: larval diet quality and plasticity in parental investment determine adult body size and male horn morphology. *Behavioural Ecology* **9**, 636–641.

Morris RF and Miller CA (1954) The development of life tables for the spruce budworm. *Canadian Journal of Zoology* **32**, 283–301.

Naeemullah M and Takeda M (1998) Selection for fast and slow development rates affected diapauses and other developmental traits in *Plodia interpunctella* (Lepidoptera: Phycitidae). *Entomological Science* **1**, 503–510.

Nijhout H, Davidowitz G and Roff D (2006) A quantitative analysis of the mechanism that controls body size in *Manduca sexta*. *Journal of Biolgy* **5**, 16.

Nylin S and Gottard K (1998) Plasticity in life history traits. *Annual Review of Entomology* **43**, 63–83.

O'Brien DM, Boggs CL and Fogel ML (2005) The amino acids used in reproduction by butterflies: a comparative study of dietary sources using compound-specific stable isotope analysis. *Physiological and Biochemical Zoology* **78**, 819–827.

Omkar and Afaq U (2013) Evaluation of Darwin's fecundity advantage hypothesis in Parthenium beetle, *Zygogramma bicolorata* Pallister. *Insect Science* **20**, 531–540.

Omkar and Pathak S (2006) Effects of different photoperiods and wavelengths of light on the life-history traits of an aphidophagous ladybird, *Coelophora saucia* (Mulsant). *Journal of Applied Entomology* **130**, 45–50.

Osawa N (1992) Sibling cannibalism in the ladybird beetle *Harmonia axyridis* Pallas: fitness consequences for mother and offspring. *Research in Population Ecology* **34**, 45–55.

Pandey P, Mishra G and Omkar (2013) Slow and fast development in Parthenium beetle and its effect on reproductive attributes. *Journal of Asia Pacific Entomology* **16**, 395–399.

Pervez A and Sharma R (2021) Influence of intraspecific competition for food on the bodyweight of the adult aphidophagous ladybird, *Coccinella transversalis*. *European Journal of Environmental Science* **11**, 5–11.

Ponsonby DJ and Copland MJW (1998) Environmental influences on fecundity, egg viability and egg cannibalism in the scale insect predator *Chilocorus nigritus*. *Biocontrol* **43**, 39–52.

Rajpurohit S, Peterson LM, Orr AJ and Marlon AJ (2016) Gibbs AG. An experimental evolution test of the relationship between melanism and desiccation survival in insects. *PLoS ONE* **11**, e0163414.

Reznik SY and Vaghina NP (2013) Effects of photoperiod and diet on diapause tendency, maturation and fecundity in *Harmonia axyridis* (Coleoptera: Coccinellidae). *Journal of Applied Entomology* **137**, 452–461.

Rotkopf R, Alcalay Y, Bar-Hanin E, Barkae ED and Ovadia O (2013) Slow growth improves compensation ability: examining growth rate and starvation endurance in pit-building antlions from semi-arid and hyper-arid regions. *Evolutionary Ecology* **27**, 1129–1144.

Schuder I, Hommes M and Larink O (2004) The influence of temperature and food supply on the development of *Adalia bipunctata* (Coleoptera: Coccinellidae). *European Journal of Entomology* **101**, 379–384.

Shafiei M, Moczek AP and Nijhout HF (2001) Food availability controls the onset of metamorphosis in the dung beetle *Onthophagus taurus* (Coleoptera: Scarabeidae). *Physiological Entomology* **26**, 173–180.

Siddiqui A, Omkar, Paul SC and Mishra G (2015) Predatory responses of selected lines of developmental variants of ladybird, *Propylea dissecta* (Coleoptera: Coccinellidae) in relation to increasing prey and predator densities. *Biocontrol Science and Technology* **25**, 992–1010.

Siddiqui A, Omkar and Mishra G (2017) Selection and inheritance of developmental variants of *Propylea dissecta* under thermal stress conditions. *Journal of Thermal Biology* **69**, 275–280.

Sih A, Cote J, Evans M, Fogarty S and Pruitt J (2012) Ecological implications of behavioural syndromes. *Ecology Letter* **15**, 278–289.

Singh N, Mishra G and Omkar (2016) Slow and fast development in two aphidophagous ladybirds on scarce and abundant prey supply. *Bulletin of Entomological Research* **106**, 347–358.

Skorping A (2007) Selecting for fast and slow maturing worms. *Proceedings in Royal Society of London B: Biological Science* **22**, 1465–1466.

Sloggett JJ and Lorenz MW (2008) Egg composition and reproductive investment in aphidophagous ladybird beetles (Coccinellidae: Coccinellini): egg development and interspecific variation. *Physiological Entomology* **33**, 200–208.

Snell-Rood EC (2013) An overview of the evolutionary causes and consequences of behavioural plasticity. *Animal Behaviour* **85**, 1004–1011.

Southwood KE (1978) Substantive theory and statistical interaction: five models. *American Journal of Society* **83**, 1154–1203.

Sundström LF and Devlin RH (2011) Increased intrinsic growth rate is advantageous even under ecologically stressful conditions in coho salmon (*Oncorhynchus kisutch*). *Evolutionary Ecology* **25**, 447–460.

Swallow JG and Garland T (2005) Selection experiments as a tool in evolutionary and comparative physiology: insights into complex traits – an introduction to the symposium. *Integrative and Comparative Biology* **45**, 387–390.

Thomas JA, Elmes W and Wardlaw JC (1998) Polymorphic growth in larvae of the butterfly *Maculinea rebeli*, a social parasite of *Myrmica* ant colonies. *Proceedings in Royal Society B: Biological Science* **265**, 1895–1901.

Ungerová D, Kalushko P and Nedvěd O (2010) Suitability of diverse prey species for development of *Harmonia axyridis* and the effect of container size. *Suitability of Diverse Prey Species for Development of Harmonia axyridis and the Effect of Container Size* **58**, 165–174.

Wcislo WT (1989) Behavioral environments and evolutionary change. *Annual Review of Ecology Evolution and Systematics* **20**, 137–169.

Zheng Y, Hagen KS, Daane KM and Miller TE (1993) Influence of larval dietary supply on the food consumption, food utilization efficiency, growth and development of the lacewing *Chrysoperla carnea*. *Entomologia Experimentalis et Applicata* **67**, 1–7.