



Does temperature modify slow and fast development in two aphidophagous ladybirds?



Neha Singh, Geetanjali Mishra, Omkar*

Ladybird Research Laboratory, Department of Zoology, University of Lucknow, Lucknow 226007, India

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ABSTRACT

Development within a population is known to vary with abiotic and biotic factors. However, instances of slow and fast development, *i.e.* different development rates within the same egg batch or cohort, have not yet been rigorously investigated in many organisms. The present study was undertaken to assess the influence of an exogenous cue, temperature (15, 20, 25, 30 and 35 °C), on slow and fast development and its effect on reproductive attributes in two ladybird species, *Menochilus sexmaculatus* (Fabricius) and *Propylea dissecta* (Mulsant) (Coleoptera: Coccinellidae). A clear bimodal pattern of distribution with two peaks was found at each temperature where the first peak represented the fast developers and the second peak slow developers. Variation in ratio and development of slow and fast developers within a cohort at different temperatures was observed to ascertain whether the phenomenon has a purely genetic basis or is environmentally influenced. The ratio of slow and fast developers in a cohort differed with temperature but not with species. Slow developers showed a female biased sex ratio and low body mass. Fast developing females laid higher numbers of eggs with higher egg viability than slow developing ones. More slow developers were found at low temperature (15 and 20 °C), equal numbers at medium temperature (25 °C) and less at higher temperature (30 and 35 °C). Results of the study are indicative of stability of the slow and fast development in the egg batch and the likelihood that the variation observed at emergence was owing to exogenous cues influenced differential rates of mortality.

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1. Introduction

Evolutionary theory predicts that fast development occurs under suitable and slow development occurs under adverse conditions (Charnov 1993; Kozłowski and Weiner 1997; Ricklefs and Wikelski 2002) including ladybirds (*e.g.* Omkar and Pervez, 2004; Omkar and Mishra, 2005; Mishra and Omkar, 2005; Omkar *et al.*, 2009). Differences in developmental rates across and between species, in response to varying environmental factors (Plaistow *et al.*, 2005; Stillwell *et al.*, 2007, 2010; Chown and Gaston 2010), have been well studied. In addition to varying in suitable and unsuitable conditions, variation in developmental and growth rate also explains size differences between the sexes in ectothermic organisms (*e.g.* Teder and Tammaru, 2005; Blanckenhorn *et al.*, 2007; Esperk *et al.*, 2007; Stillwell *et al.*, 2007, 2010) and mammals (*e.g.*, the slow–fast continuum) (Heppell *et al.*, 2000; Ricklefs, 2000; Sæther and Bakke, 2000; Fisher *et al.*, 2001; Bennett and Owens, 2002; Oli, 2004; Bielby *et al.*, 2007). Gouws *et al.* (2011) in a study of 57 insect species found that intraspecific body size frequency distributions in a localized area, are commonly bimodal in social insects (24 out of 30 species), and less common but still present

in other insect orders. These size variations could be a result of differences in developmental rate since there is a strong correlation between body size and development (Katvala and Kaitala, 2001; Roff, 2002; Thorne, *et al.*, 2006; Omkar and Afaq, 2012).

Genetic variation in phenotypic plasticity for developmental rates and size in sub-populations has been used as a tool in selecting for faster developing organisms as is in the case of *Drosophila melanogaster* (Meigen) (Partridge and Fowler 1992), ladybird, *Hippodamia convergens* (Guérin-Méneville) (Rodríguez-Saona and Miller, 1995) and a lepidopteran, *Manduca sexta* (Linnaeus) (D'Amico *et al.*, 2001).

However, the phenomenon of discrete developmental or growth rate polymorphisms, that is the coexistence of two significantly different developmental rates within a cohort or an egg batch of a mother, is much less investigated. There have been a few studies addressing dramatic examples of growth rate polymorphism; for example, the myrmecophilous butterfly *Maculinea rebeli* Hirschke (Thomas *et al.*, 1998; Schonrogge *et al.*, 2000; Nowicki *et al.*, 2005; Witek *et al.*, 2006), the predaceous syrphid, *Microdon mutabilis* (Linnaeus) (Schonrogge *et al.*, 2000) and a salmonid fish (Gross, 1985). In *M. rebeli*, 25% of the population within a cohort developed in a year, while the rest took two years. The subtle variations of this phenomenon have also been mentioned in the ladybirds *Adalia bipunctata* (Linnaeus) (Dixon, 2000)

* Corresponding author.

E-mail address: omkaar55@hotmail.com (Omkar).

and *Harmonia axyridis* (Pallas) (Grill et al., 1997), but it is only recently that the existence of this polymorphism has been established in the ladybirds *Menochilus sexmaculatus* (Fabricius) and *Propylea dissecta* (Mulsant) (Mishra and Omkar, 2012). Mishra and Omkar (2012) found a clear bimodal pattern of distribution of developmental rates within a cohort in both ladybird species. The ratio of slow to fast developers was similar in both species and was unaffected by the sex of the developing individuals. The slow and fast developers were found to differ significantly not only in their rate of development but also in their reproductive attributes. Those findings raise questions regarding the constancy of these variants across organisms and whether the ratios of the developmental rate variants within the cohorts were genetically determined or influenced by exogenous cues. It is to examine the effect of exogenous cues on the ratio of slow:fast developers that the present study has been designed.

Temperature was selected as the most likely exogenous cue since it is one of the most critical factors influencing development (Ernsting and Isaaks, 2000; Davidowitz et al., 2004, 2005; Davidowitz and Nijhout, 2004; Plaistow et al., 2005), predation and oviposition rates of various organisms including ladybirds (Hodek and Honek, 1996; Obrycki and Kring, 1998; Hodek et al., 2012). Temperature-driven models have been used to predict rates of development (Roy et al., 2002), and seasonal incidence (Briere and Pracros, 1998) and to suggest suitable conditions for the mass rearing of ladybirds (Orr and Obrycki, 1990; Rodriguez-Saona and Miller, 1999; Srivastava and Omkar, 2003; Pervez and Omkar, 2004). If the slow-growth-high mortality hypothesis (Johnson and Gould, 1992) holds true, then selection would favour emergence of more fast developers in cohorts under slow developing conditions.

This study examines the existence and consistency of slow and fast development ratios under five temperatures in two aphidophagous ladybirds, *M. sexmaculatus* and *P. dissecta* (Coleoptera: Coccinellidae). We hypothesize that this bimodality is genetically based, but also modified by temperature induced mortality.

The results of this study could lay the foundation for further studies, contributing to the identification of slow and fast development in more ladybird species and understanding the ecological and evolutionary reasons for its occurrence. On the applied front, it could help in the selection of fast developing lines and thereby assist in the mass production of predatory ladybirds, an important group of bioagents for various pest species.

2. Materials and methods

2.1. Organisms

Two locally abundant predaceous ladybird species, viz. *M. sexmaculatus* and *P. dissecta*, were selected primarily owing to their fast development and prominent size variations and because a previous study on development rate polymorphism (Mishra and Omkar, 2012) was conducted in these ladybirds.

2.2. 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 aphid, *Aphis craccivora* (Koch) on the host plant *Vigna unguiculata* (L.) (raised from glasshouse cultures; 21 ± 1 °C; 65 ± 5% R.H.) under standard laboratory conditions (27 ± 1 °C; 65 ± 5% R.H.; 14 L: 10D). Eggs laid were collected every 24 h and incubated under the conditions above until hatching. The larvae were reared until adult emergence in plastic beakers (14.5 × 10.5 cm²; 5 instars per

beaker). The requisite stages were taken from the stock culture for experiments.

2.3. Experimental design

2.3.1. Existence of slow and fast developers

Ten pairs of 10-day-old unmated adults were paired in separate plastic Petri dishes (size and prey as above) and placed at each one of the five temperatures, (15, 20, 25, 30 and 35 °C). Two hundred and forty eggs from the first five days of egg laying by *M. sexmaculatus* and *P. dissecta* were separated and placed at the same temperature as their parents. Hatched instars were isolated and placed individually in the Petri dishes described above, observed for molting twice a day and reared until adult emergence. They were provided with second and third instars of *A. craccivora* at 30 mg for L₁ and L₂ and at 50 mg for L₃, L₄ and adults. The instars were grouped as slow and fast developers on the basis of their total developmental period following (Mishra and Omkar, 2012). The mass of emerging adults was measured 6 h after molting. The percentage of immature survival (number of adults emerged/number of first instars × 100), slow:fast emergence ratio (number of slow or fast developers/total individuals emerged) and sex ratio (number of females in slow or fast developers/total number of slow or fast developers) was also calculated for each species at each temperature.

2.3.2. Effect of slow-fast development on reproductive attributes

The newly emerged adults of each development time variant were paired in Petri dishes (size as above) and provided with aphid, *A. craccivora*. Daily oviposition was recorded for the next 20 days and egg viability was recorded for 15 pairs from each variant (i.e. slow and fast) at each temperature (15, 20, 25, 30 and 35 °C).

2.4. Statistical analysis

Data on total developmental duration (from day of egg laying to adult emergence) for each species at each temperature were subjected to Kolmogorov–Smirnov tests of normality to assess for normal distribution. The overall distribution of developmental durations of *M. sexmaculatus* and *P. dissecta* was not normal (Table 1). The frequencies of the developmental durations were graphed and shown a clear bimodal pattern (Fig. 1). Based on the

Table 1
Normality of developmental duration at different temperatures for *M. sexmaculatus* and *P. dissecta*.

Temperature(°C)	Species	Normality of data
15	<i>M. sexmaculatus</i>	D+: 0.171 D-: 0.075 D: 0.171; P-Value < 0.01
	<i>P. dissecta</i>	D+: 0.179 D-: 0.099 D: 0.179; P-Value < 0.01
20	<i>M. sexmaculatus</i>	D+: 0.078 D-: 0.080 D: 0.080; P-Value < 0.01
	<i>P. dissecta</i>	D+: 0.079 D-: 0.077 D: 0.079; P-Value: 0.013
25	<i>M. sexmaculatus</i>	D+: 0.083 D-: 0.080 D: 0.083; P-Value < 0.01
	<i>P. dissecta</i>	D+: 0.087 D-: 0.080 D: 0.087; P-Value < 0.01
30	<i>M. sexmaculatus</i>	D+: 0.078 D-: 0.072 D: 0.078; P-Value < 0.01
	<i>P. dissecta</i>	D+: 0.171 D-: 0.075 D: 0.171; P-Value < 0.01
35	<i>M. sexmaculatus</i>	D+: 0.078 D-: 0.072 D: 0.078; P-Value < 0.01
	<i>P. dissecta</i>	D+: 0.085 D-: 0.082 D: 0.085; P-Value < 0.01

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