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Optimization of age difference between mates maximizes reproductive output

Omkar · Geetanjali Mishra

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Abstract The influence of the age difference between mates on the reproductive output of an aphidophagous ladybird, *Propylea dissecta* (Mulsant) (Coleoptera: Coccinellidae) was studied. This was done by varying the ages of either the males or females and keeping that of the other sex constant. The optimum age difference for maximum reproductive output was also identified. This study is the first attempt in insects. Pairs in which the female was five days older than the male resulted in the highest number of progeny. The number of progeny produced in this pair was however not statistically different from pairs in which females were 0 and 10 days older than the males. Synchronization between age-specific daily oviposition and viability trends was observed in groups with high reproductive output. Asynchronization amongst male and female ageing trajectories was found responsible for the reduced reproductive output. This study reveals that if the female is 5–10 days older than the male at a young age, then there is increased likelihood of production of maximum number of progeny.

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Omkar (✉) · G. Mishra
Ladybird Research Laboratory, Department of Zoology, University of Lucknow, Lucknow 226007, India
e-mail: omkaar55@hotmail.com

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Introduction

Ageing in all organisms leads to a decline in virtually all demographic, behavioral and physiological parameters (Finch 1990; Rose 1991). In insects, ageing influences mate choice (Beck and Powell 2000; Hansen and Price 1995; Jones et al. 2000; Kokko and Lindstrom 1996), mating incidences (Hemptinne et al. 2001; Omkar and Pervez 2005; Srivastava and Omkar 2004), mating duration (Martin and Hosken 2002), daily oviposition (Dixon and Agarwala 2002; Kindlmann et al. 2001; Novoseltsev et al. 2003; Omkar et al. 2004), predation (Veeravel and Baskaran 1995), selectivity (Fréchette et al. 2004) and fertility, rate of assimilation and speed of locomotion (Dixon and Agarwala 2002). Increase in female age beyond prime results in decline in fecundity (Begon and Parker 1986; Foster and Howard 1999; Mishra and Omkar 2004; Navasero and Elzer 1992; Omkar and Singh 2005; Pervez et al. 2004; Srivastava and Omkar 2004). On the other hand, increasing age in males leads to declining levels of fertility beyond a certain age (Fox et al. 1995; Mishra and Omkar 2004; Pervez et al. 2004; Srivastava and Omkar 2004). Numerous studies on ageing in terms of mortality

trajectories show that the rates of mortality increase with age (see Robine 2001). Ageing trajectories in female and male ladybirds have also been studied in terms of change in daily oviposition and percent egg viability (Mishra and Omkar 2006). Age-specific trends in daily oviposition were found indicative of female ageing while the age-specific viability graphs were strongly correlated with male ageing in the ladybird, *Propylea dissecta* (Mulsant) (Mishra and Omkar 2006).

Previous studies reveal that the age at which gonadal maturation takes place in the two sexes differs in many insects. In insects, the early maturation of testicular follicles over ovarioles has been recorded (Nunney 1996; Reed and Beckage 1997). This has also been recorded in some ladybirds, where male pupae possess mature gonads (Ceryngier et al. 1992; Isogai et al. 1990), while the female gonads mature only after emergence (Dixon 2000). However, *Adalia bipunctata* (Linnaeus) is slightly protogynous, but the difference is not thought to be significant (Hemptinne et al. 2001). The females of this beetle were however found to mate earlier than the males (Hemptinne et al. 2001).

The effect of age on many physiological activities of insects viewed along with the differences in age at gonadal maturation in the two sexes leads to the postulation that the onset of senescence and ageing rates in males and females are also likely to differ. This has been recently reported in *P. dissecta* (Mishra and Omkar 2006). A lack of coincidence in peaks of male and female fitness has been previously suggested and investigated (Arnqvist and Nilsson 2000; Arnqvist and Rowe 2002).

These observed differences in ageing rates or the attainment of male and female optima could thus affect the progeny production in ladybirds depending on the age difference (AD) between the mates. Differences in the ages of the sexes are thought to be important in reproduction and sexual selection (Mack et al. 2003). This is also ecologically relevant because: (a) there is overlap between successive generations of ladybirds, and (b) they move between patches of prey, thus encounters between individuals of different ages is likely.

The aim of this study was thus to identify the effect of age difference on progeny production and to understand the mechanism behind it by comparing male and female ageing trajectories. This, to the best of our knowledge, is the first attempt to study the effect of differences in the ages of paired sexes on progeny production in insects. For this an aphidophagous ladybird, *P. dissecta*, of Oriental origin, commonly found in the vicinity of crops infested with aphids, *Aphis craccivora* Koch and *Aphis gossypii* Glover (Omkar and Pervez 2004) was used. A major reason for selecting this species is its marked sexual dimorphism in the structure of the pronotum (Omkar and Pervez 2000), which made it easy to identify the sexes.

Materials and methods

Stock culture

Adults of *P. dissecta,* collected from agricultural fields close to Lucknow (India), were fed an ad libitum supply of the aphid, *A. craccivora* reared on *Dolichos lablab* Linnaeus under controlled laboratory conditions (25 ± 2°C; 65 ± 5% R.H.; 14L: 10D) and their oviposition monitored. The larvae that hatched from the eggs were reared in muslin-covered beakers containing an ad libitum supply of prey (as above). On emergence the adults were isolated and sexed on the basis of specific pronotal patterns (Omkar and Pervez 2000) and a note kept of their age (24 h after emergence = 1-day-old). All experiments were conducted under conditions similar to those experienced by the stock culture.

Experimental design

The age differences between paired sexes were obtained by varying either the male (experiment-I) or female (experiment-II) age.

(I) Varying male age

Males of different ages, viz. 0 (6-h-old), 5, 10, 15, 20, 25, 30, 35, 40, 45, 50, 55, 60 and 65 days were paired for life with five-days-old females in Petri dishes. This resulted in age differences of −5 days, 0 (same age), +5, +10, +15, +20, +25, +30, +35, +40, +45, +50, +55, and +60 days, respectively. A negative (−) sign indicates the female is older and positive (+) sign that the male is older. Five-day-old females were used because they were receptive to male advances and readily mated (Omkar and Pervez 2005). Males

up to the ages of 65 days were used as they are known to have longevity of 121.6 ± 3.3 days when unmated. Decrease in lifespan of males is negatively correlated to the number of matings (Mishra and Omkar 2006).

Each pair was provided daily with a fresh ad libitum supply of *A. craccivora*. Twenty pairs per age combination were formulated to overcome instances of no mating between pairs and premature death (within 10 days of mating) of an individual. Such cases were excluded and data from ten replicates only were analyzed. A pair of individuals in a Petri dish whose first mating had been visually confirmed constituted a replicate. Each pair was kept together for their lifetime and the pre-oviposition (days from pairing to first oviposition), oviposition (first to last day of oviposition), and post-oviposition (day after last oviposition till death of female) periods, daily oviposition, daily percent egg viability and lifetime fecundity and viability (absolute viability) of eggs were recorded. The daily oviposition and percent egg viability were used for mapping female and male ageing trajectories, respectively. These were used for comparing the synchrony amongst daily egg laying and hatching patterns in pairs with different age differences. Details of this analysis are given in the section on statistical analysis.

(II) Varying female age

In this experiment, the age of the females varied (from 0 to 65 days) and the males were all initially five days old, an age at which they readily mate. This resulted in age difference of the pairs of +5 days, 0 (same age), −5, −10, −15, −20, −25, −30, −35, −40, −45, −50, −55, and −60 days, respectively. The signs, as above indicate the relative ages of the two sexes in each pair. Unmated females of the maximum age of 65 days were used in the study as their longevity has been found to be up to 125.2 ± 4.1 days (Mishra and Omkar 2006). Prey was provided and replicates formulated as described above. The pre-oviposition, oviposition, and post-oviposition periods, daily oviposition and viability of the eggs laid in a day were recorded.

Statistical analysis

Equality of variances was checked using Bartlett's test and variances appear to be statistically equal. The data were analyzed in two steps to understand: (1) the overall lifetime effect of age differences on reproductive output, and (2) the probable reason behind this influence.

To fulfill the first statistical objective, data on pre-oviposition, oviposition, and post-oviposition periods, fecundity (lifetime oviposition), % viability (% total eggs that hatched or absolute viability), male and female longevity (from emergence to death) were subjected to one-way ANOVA using statistical software SAS (2002) and the differences between means of activity were calculated using post hoc Tukey's honest significance test to observe the overall effect of age differences between mates. All the percentage data were Arcsin square root transformed prior to being subjected to ANOVA.

To fulfill the second objective, the daily oviposition and its corresponding egg viability was used. Firstly, the data were pooled into groups based on arbitrarily selected criteria. The male optima (last day of 95% egg viability) and female optima (day of maximum oviposition or peak) of all AD categories were subjected to ANOVA. The selection of these optima was arbitrary and decided upon after thorough study of the organisms' biology. Last day of 95% egg viability was selected as male optima because (a) viability differed significantly when male age varied, and (b) egg batches laid in a day by a single female of *P. dissecta* quite routinely achieve 95% egg viability for up to a continuous stretch of 10–15 days on a diet of *A. craccivora* at 27°C. Day of peak oviposition was selected as female optima because (a) fecundity differed significantly when female age varied, and (b) female ladybirds including *P. dissecta* show triangular fecundity function with a peak of oviposition (Omkar and Mishra 2005).

In experiment-I, male optima was found to differ significantly, while in experiment-II female optima differed significantly. The data on daily oviposition and % viability of daily oviposited eggs of AD categories that did not show statistically significant differences were pooled into groups for the purpose of easy plotting, removal of the overlapping of data and better interpretation (Fig. 1).

Based on the above criteria, pairs from experiment-I were pooled into five groups: Group 1 (AD − 5 to 0 days; male optima achieved between 20 and 25th day of pairing), Group 2 (AD +5 to +10 days; 15–19th day of pairing), Group 3 (AD +15 to

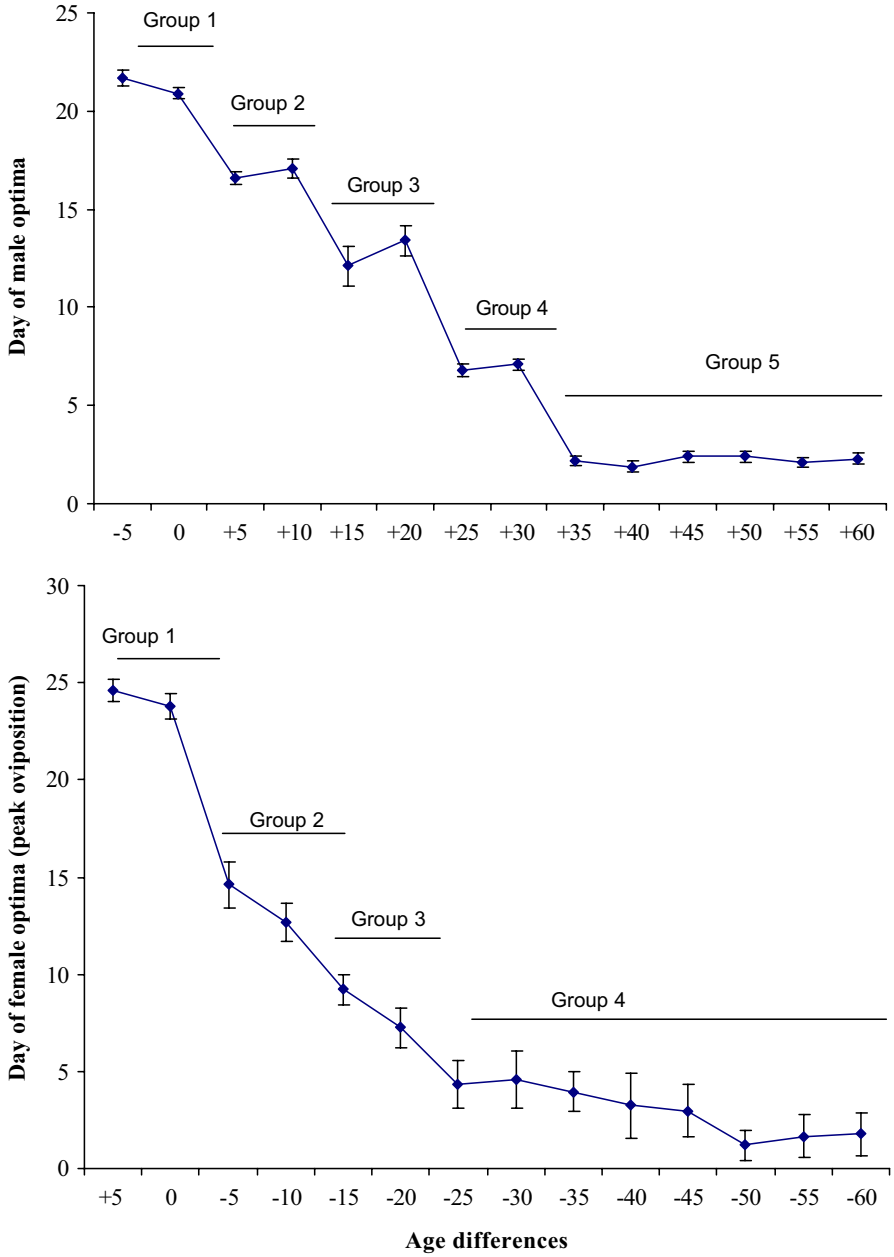

Fig. 1 Criteria for formulation of groups based on **a** day of male optima when male age varied and **b** day of female optima when female age varied. Values are mean ± SE

+20 days; 10–14th day of pairing), Group 4 (AD +25 to +30 days; 5–9th day of pairing), and Group 5 (AD +35 to +60 days; 1–4th day of pairing).

In experiment-II, four groups were formulated: Group 1 (AD +5 to 0 days; female optima between 20 and 25th day of pairing), Group 2 (AD −5 to −10 days; 10–15th day, Group 3 (AD −15 to −20 days; 5–10th day) and Group 4 (AD −25 to −60 days; 1–5th day).

The ageing trajectories of both male and female *P. dissecta* of the above formulated groups were plotted. The female ageing trajectory is formulated by mapping daily oviposition by the female for a lifetime, while male ageing trajectory is plotted by mapping percent viability of a day's oviposition (Mishra and Omkar 2006) and the two trends were compared visually as well as statistically for synchronization.

These ageing trajectories were subjected to polynomial regression against reproductive age. The regression coefficients were compared using SAS

(2002) with the null hypothesis H_o: $r_{female} = r_{male}$, where r_{female} is the regression coefficient for females and r_{male} is the regression coefficient for males. For this analysis a dummy variable was created in which females were coded 1 and males 0. The regression coefficients were compared and the *t*-values obtained through Fisher's exact t-test indicated differences, if any, in the ageing trajectories of both the sexes. This allowed interpretation of the synchronization or the absence of it in these trends. Fecundity trends of the respective groups in both parts of the study were appraised for their role in progeny production by comparing their regression coefficients by non-parametric Kruskal–Wallis test of significance. The same was repeated with egg viability in both parts of the study.

Results

(I) Varying male age

Results following ANOVA reveal that variations in lifetime fecundity in relation to age differences formed by varying male age were not significant ($F = 3.45$; $P = 0.25$; $df = 13, 126$; Fig. 2) and did not show a trend. Lifetime or absolute percent egg viability decreased significantly with increase in the age difference ($F = 207.75$; $P < 0.001$; $df = 13, 126$) and was highest when the females were paired with newly emerged males, i.e., AD (−5). Differences in pre- ($F = 1.38$; $P = 0.31$; $df = 13, 126$) and post-oviposition ($F = 2.24$; $P = 0.09$; $df = 13, 126$) periods were statistically non significant (Fig. 2). Differences in age did not significantly alter the oviposition period ($F = 1.27$; $P = 0.22$; $df = 13, 126$; Fig. 2). The variation in longevity of males was statistically significant ($F = 16.21$; $P < 0.01$; $df = 13, 126$; Fig. 2).

Visual interpretation of the trends in the five formulated groups revealed prominent lack of synchronization among the fecundity and viability trends of Groups 3, 4, and 5 from the middle to the later part of life (Fig. 3). There seems to relative synchronization in Group 2 for a major part of life with asynchronization visible only in the very end part of life. Group 1 was found to show peaks and troughs at the same part of life with the same increase as well decline rates and was thus visually most synchronized. To corroborate visual interpretation, statistical analysis of age-specific daily fecundity and viability trends in the five formulated groups (each group with homogeneous male optima) by regression analysis and comparison of regression coefficients was done. This revealed that there was no statistically significant differences in the coefficients ($t = 1.25$; $P = 0.23$; $df = 1$; Table 1) of Group 1 indicating synchronization in the daily fecundity and daily relative viability. However, significant differences were found in the regression coefficients of the other four groups, viz. Group 2 ($t = 2.52$; $P < 0.05$; $df = 1$; Table 1; Fig. 3), Group 3 ($t = 3.99$; $P < 0.01$; $df = 1$; Table 1; Fig. 3), Group 4 ($t = 5.07$; $P < 0.001$; $df = 1$; Table 1; Fig. 3) and Group 5 ($t = 13.23$; $P < 0.001$; $df = 1$; Table 1; Fig. 3).

The visual interpretation as well as statistical analysis reveals that the differences in ageing trajectories of males and females, i.e., trends of age-specific daily fecundity and viability, respectively, were insignificant in Group 1 indicating that the two trends were coincident, while the same was not true for the other four groups.

Comparison of fecundity trends indicated lack of significant differences ($H = 0.99$; $P = 0.33$; $df = 4$), while the trends of age-specific egg viability showed significant differences ($H = 7.00$; $P < 0.001$; $df = 4$; Table 2) indicating progeny production to be entirely dependent on egg viability when male age was varied.

(II) Varying female age

Results reveal that variations in lifetime or absolute fecundity in relation to age difference formed by varying female age was significant ($F = 26.10$; $P < 0.001$; $df = 13, 126$; Fig. 4) but did not show any specific trend. Differences in pre- ($F = 107.37$; $P < 0.001$; $df = 13, 126$; Fig. 4) and post-oviposition periods were statistically significant ($F = 62.53$; $P < 0.001$; $df = 13, 126$; Fig. 4). Variation in age differences significantly affected the oviposition period ($F = 558.09$; $P < 0.001$; $df = 13, 126$; Fig. 4). Fecundity too varied significantly with increase in female age ($F = 558.04$; $P < 0.001$; $df = 13, 126$; Fig. 4) and showed an initial increase up to the age of AD +5 (female older) followed by a decrease. The longevity of females varied significantly ($F = 23.47$; $P < 0.001$; $df = 13, 126$; Fig. 4).

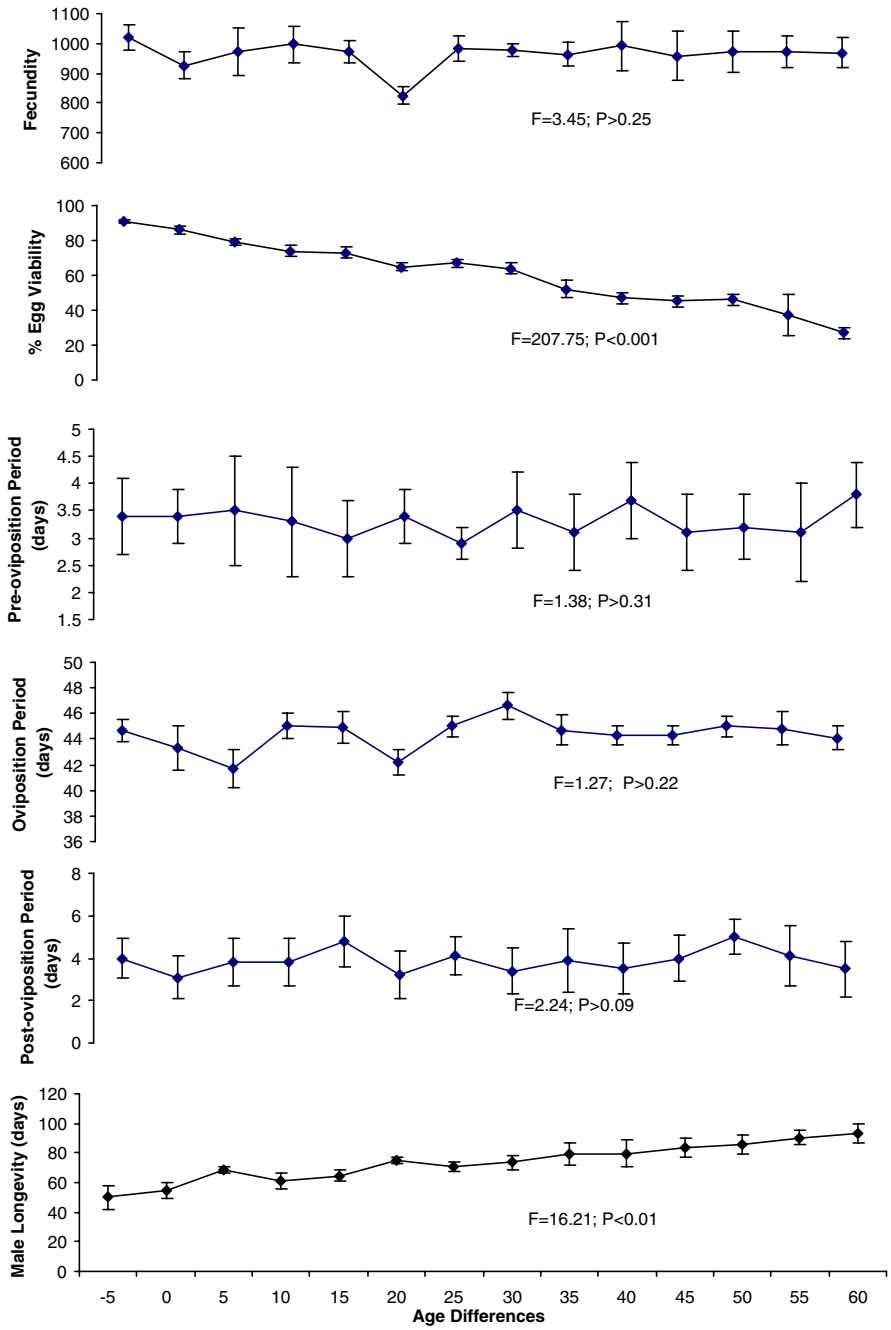

Fig. 2 Effect of age differences at varying male age on certain life attributes of *P. dissecta*. Longevity values are inclusive of days unpaired. Values are mean ± SE. NS stands for statistically non significant data. Tukey's test range = 4.84; *df* = 13, 116

A visual perusal of the age-specific daily fecundity and viability trends in the four groups was done. Very prominent asynchronization was visible in Groups 3 and 4. While the viability remained high in these groups there was a prominent decline in daily fecundity leading to reduced progeny production. However, the trends in Groups 1 and 2 seem quite highly synchronized. Statistical analysis of the trends through comparison of regression coefficients of age-specific daily fecundity and viability in the four groups formulated on the basis of when the females were at their optimum (each group was homogeneous in this respect) was done. This analysis revealed non significant differences

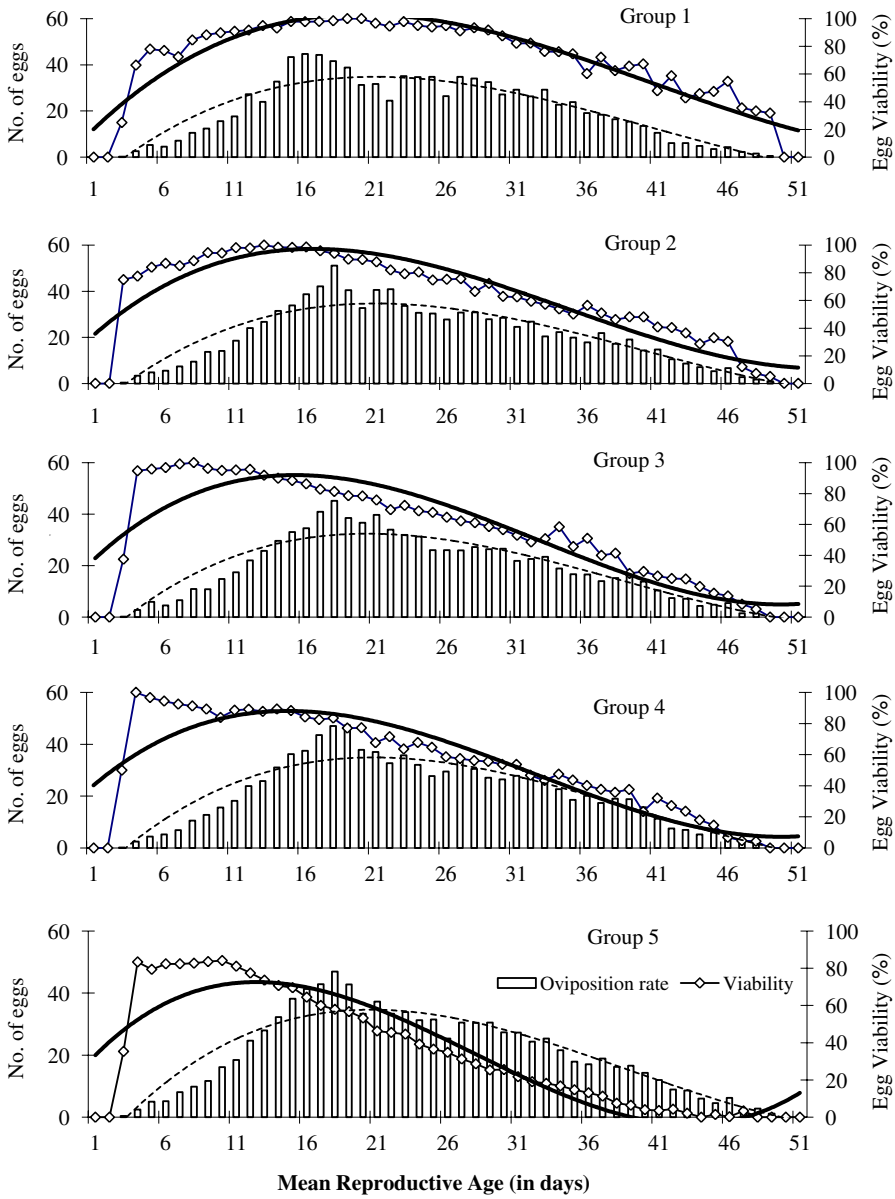

Fig. 3 Presence or absence of synchronization of age-specific oviposition and viability trends at different age differences formed by varying male age. Dashed and bold line depicts oviposition and egg viability trends, respectively

between coefficients of daily fecundity and viability trends in Group 2 ($t = 1.61$; $P = 0.37$; $df = 1$) and Group 1 ($t = 1.92$; $P = 0.07$; $df = 1$) indicating synchronization in the fecundity and viability trends of both these groups across the ladybirds reproductive period. However, significant differences were found in regression coefficients of the other two groups, viz. Group 3 ($t = 3.87$; $P < 0.01$; $df = 1$; Table 1; Fig. 5) and Group 4 ($t = 6.91$; $P < 0.001$; $df = 1$; Table 1; Fig. 5). Thus, the daily fecundity and viability trends in Groups 1 and 2 were largely coincident. However, owing to higher fecundity in Group 2 the overall progeny output was higher.

Comparison of fecundity ($H = 11.25$; $P < 0.001$; $df = 4$; Table 3) and viability ($H = 3.25$; $P < 0.05$; $df = 4$; Table 3) trends showed significant differences indicating the role of both of these in progeny production when female age was a varying factor.

Table 1 Comparison of regression trends of age-specific fecundity (eggs laid) and viability (eggs hatched) in the various groups formed for the study of age differences

Groups	Parameters	Regression equations	r	P	Comparison of equations (t-value)
Male age variance					
Group 1	Fecundity	$Y = -0.0636X^2 + 3.1191X - 5.206$	0.8113	<0.001	1.25 ($P = 0.23$; $df = 1$)
	Viability	$Y = -0.0593X^2 + 2.8407X - 4.1344$	0.7941	<0.001	
Group 2	Fecundity	$Y = -0.0618X^2 + 3.0473X - 4.7825$	0.8094	<0.001	2.52 ($P < 0.05$; $df = 1$)
	Viability	$Y = -0.0489X^2 + 2.2589X - 0.2614$	0.6594	<0.001	
Group 3	Fecundity	$Y = -0.0575X^2 + 2.8002X - 3.8734$	0.796	<0.001	3.99 ($P < 0.01$; $df = 1$)
	Viability	$Y = -0.0392X^2 + 1.7569X + 1.468$	0.6574	<0.001	
Group 4	Fecundity	$Y = -0.0629X^2 + 3.0969X - 5.1544$	0.8134	<0.001	5.07 ($P < 0.001$; $df = 1$)
	Viability	$Y = -0.041X^2 + 1.8506X + 0.9906$	0.6445	<0.001	
Group 5	Fecundity	$Y = -0.0613X^2 + 3.0025X - 4.3169$	0.8046	<0.001	13.23 ($P < 0.001$; $df = 1$)
	Viability	$Y = -0.0239X^2 + 0.9637X + 4.4799$	0.5201	<0.01	
Female age variance					
Group 1	Fecundity	$Y = -0.0603X^2 + 2.7548X - 1.3665$	0.6529	<0.001	1.92 ($P = 0.07$; $df = 1$)
	Viability	$Y = -0.0597X^2 + 2.6811X - 2.1125$	0.7041	<0.001	
Group 2	Fecundity	$Y = -0.0372X^2 + 1.2778X + 17.181$	0.7864	<0.001	1.61 ($P = 0.37$; $df = 1$)
	Viability	$Y = -0.0383X^2 + 1.3489X + 14.088$	0.7687	<0.001	
Group 3	Fecundity	$Y = -0.0044X^2 - 1.0218X + 38.715$	0.8524	<0.001	3.87 ($P < 0.01$; $df = 1$)
	Viability	$Y = -0.0195X^2 - 0.2121X + 27.402$	0.7704	<0.001	
Group 4	Fecundity	$Y = 0.0299X^2 - 1.8024X + 29.657$	0.9825	<0.001	6.91 ($P < 0.001$; $df = 1$)
	Viability	$Y = 0.0067X^2 - 0.8196X + 19.438$	0.8504	<0.001	

The null hypothesis H_o: $r_{female} = r_{male}$, where r_{female} and r_{male} are regression coefficients of female and male trajectory, respectively. This was tested with a dummy variable having female = 0 and male = 1. The letter X in the regression equation stands for age, while Y stands for fecundity and viability in equations for female and male trajectory, respectively

Table 2 Comparison of regression trends of age-specific fecundity and viability in the various groups formed for the study of age differences by varying male age

Groups	Regression equations	r	P	Comparison of coefficients (H-value)
Fecundity				
Group 1	$Y = -0.0636X^2 + 3.1191X - 5.206$	0.8113	<0.001	$H = 0.99$ ($P = 0.33$; $df = 4$)
Group 2	$Y = -0.0618X^2 + 3.0473X - 4.7825$	0.8094	<0.001	
Group 3	$Y = -0.0575X^2 + 2.8002X - 3.8734$	0.796	<0.001	
Group 4	$Y = -0.0629X^2 + 3.0969X - 5.1544$	0.8134	<0.001	
Group 5	$Y = -0.0613X^2 + 3.0025X - 4.3169$	0.8046	<0.001	
Viability				
Group 1	$Y = -0.0593X^2 + 2.8407X - 4.1344$	0.7941	<0.001	$H = 7.00$ ($P < 0.001$; $df = 4$)
Group 2	$Y = -0.0489X^2 + 2.2589X - 0.2614$	0.6594	<0.001	
Group 3	$Y = -0.0392X^2 + 1.7569X + 1.468$	0.6574	<0.001	
Group 4	$Y = -0.041X^2 + 1.8506X + 0.9906$	0.6445	<0.001	
Group 5	$Y = -0.0239X^2 + 0.9637X + 4.4799$	0.5201	<0.01	

The letter X in the regression equation stands for age, while Y stands for fecundity and viability in equations for female and male trajectory, respectively. The regression coefficients were compared using non-parametric Kruskal–Wallis test of significance

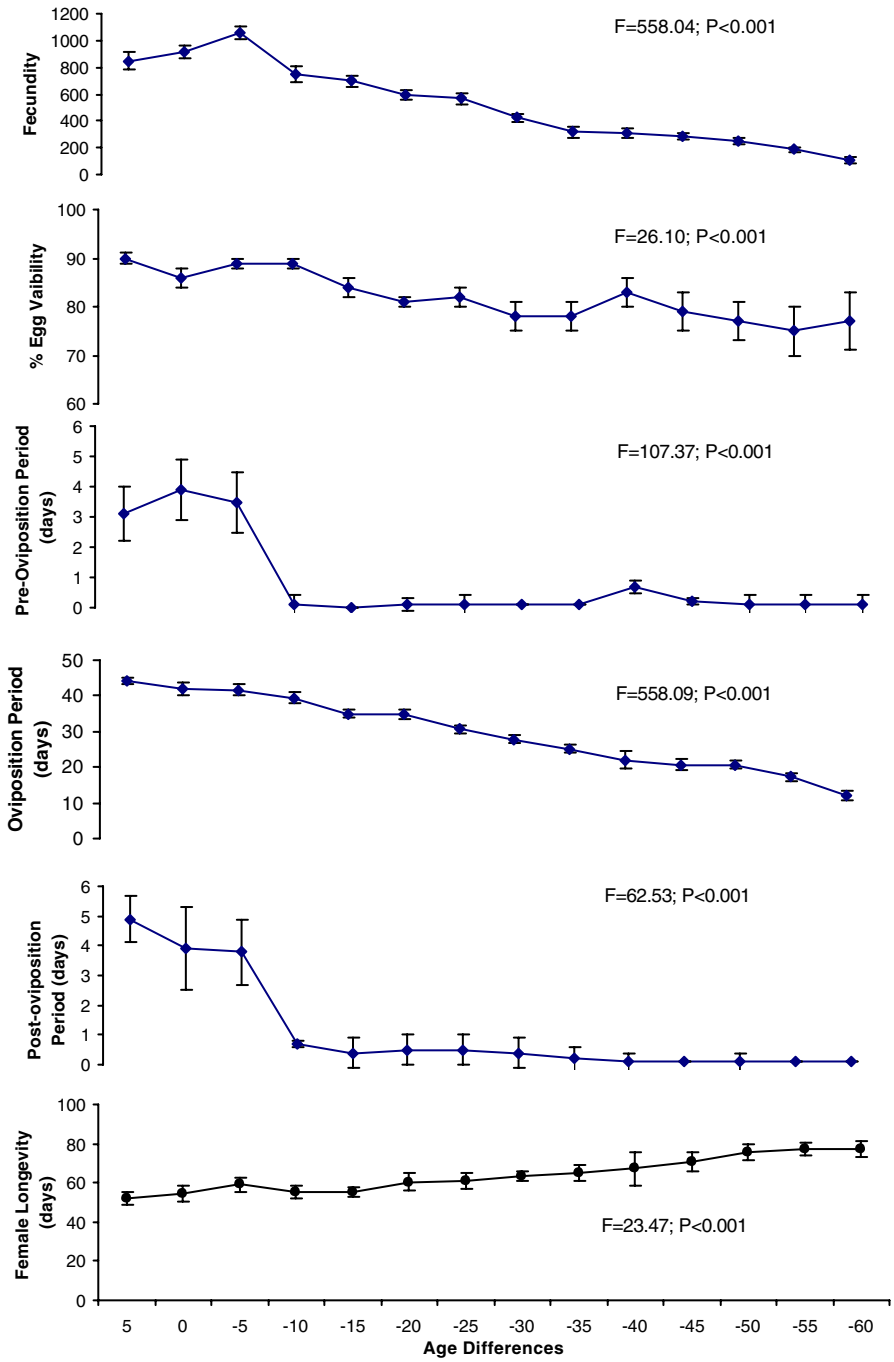

Fig. 4 Effect of age differences at varying female age on certain life attributes of *P. dissecta*. Longevity values are inclusive of days unpaired. Values are mean ± SE. NS stands for statistically non significant data. Tukey's test range = 4.84; $df = 13, 116$

Discussion

The effect of differences in the age of mates on reproductive output has not, to the best of our knowledge, been previously studied in insects. The results of the experiments reported here clearly reveal that age as well as age differences have a significant effect on the overall progeny production.

The observations of the present study were analyzed at two different levels. Interpretation of the effect of age differences on the lifetime reproductive output of *P. dissecta* reveals that highest lifetime

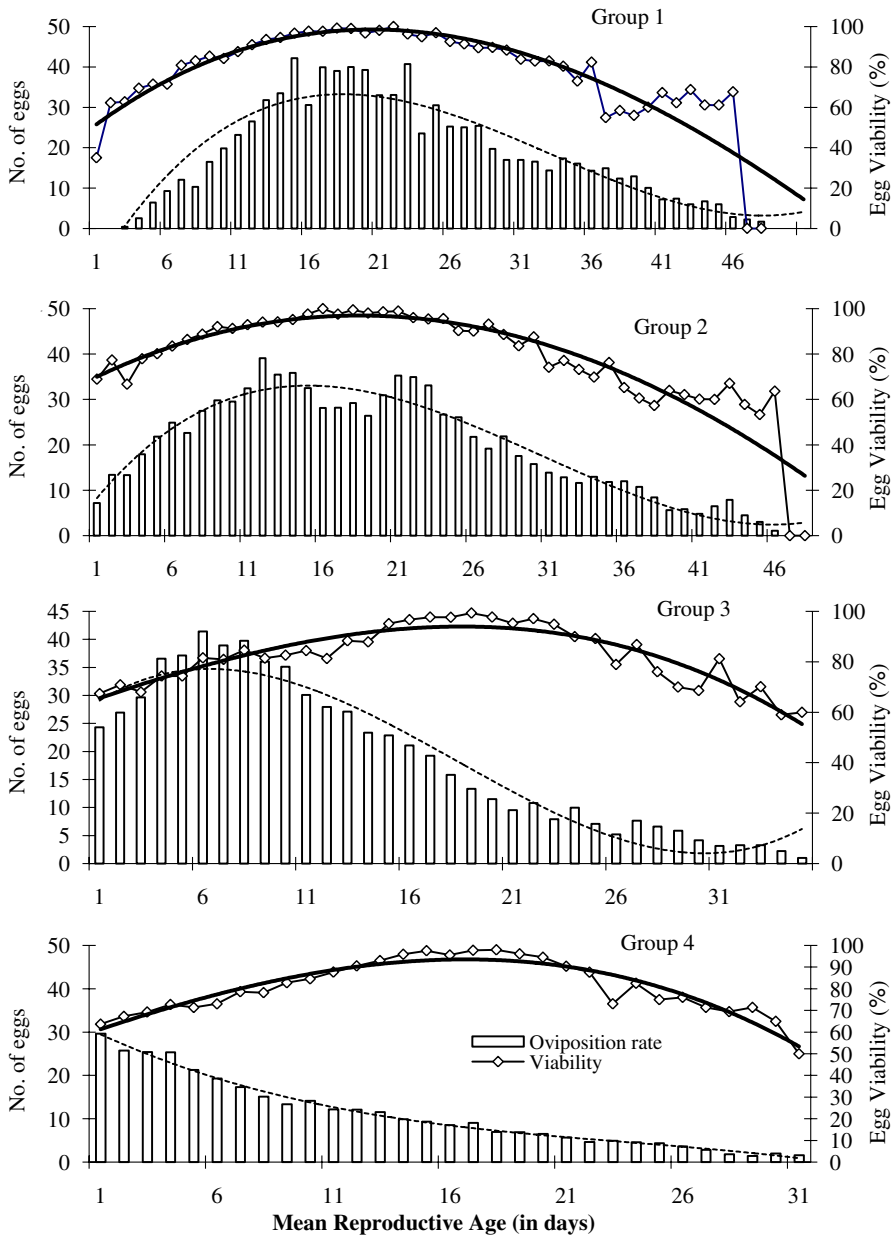

Fig. 5 Presence or absence of synchronization of age-specific oviposition and viability trends at different age differences formed by varying female age. Dashed and bold line depicts oviposition and egg viability trends, respectively

viability was obtained when males were taken into pairs as newly emerged or at a younger age. The highest fecundity was on the other hand obtained when the females were taken into pairs at the age of about 10 days. This indicates that pairing of older females with younger males would probably result in higher reproductive output. To avoid the trend of declining viability as a result of male ageing it would probably be more feasible to replace the ageing males with young males in a stock culture as well in mass multiplication units. Though the results indicate that pairs having females 5–10 days older than males at early ages would be the best combination for high progeny output, however, to safely state this we would need a full matrix of various ages of both sexes and not only the two sets (one row and one column) used in the present study.

Analysis of the ageing trajectories to interpret the reasons behind the differing progeny output with age differences revealed that it was the presence or

Table 3 Comparison of regression trends of age-specific fecundity and viability in the various groups formed for the study of age differences by varying female age

Groups	Regression equations	r	P	Comparison of coefficients (H-value)
Fecundity				
Group 1	$Y = -0.0603X^2 + 2.7548X - 1.3665$	0.6529	<0.001	$H = 11.25$ ($P < 0.001$; $df = 4$)
Group 2	$Y = -0.0372X^2 + 1.2778X + 17.181$	0.7864	<0.001	
Group 3	$Y = -0.0044X^2 - 1.0218X + 38.715$	0.8524	<0.001	
Group 4	$Y = 0.0299X^2 - 1.8024X + 29.657$	0.9825	<0.001	
Viability				
Group 1	$Y = -0.0597X^2 + 2.6811X - 2.1125$	0.7041	<0.001	$H = 3.25$ ($P < 0.05$; $df = 4$)
Group 2	$Y = -0.0383X^2 + 1.3489X + 14.088$	0.7687	<0.001	
Group 3	$Y = -0.0195X^2 - 0.2121X + 27.402$	0.7704	<0.001	
Group 4	$Y = 0.0067X^2 - 0.8196X + 19.438$	0.8504	<0.001	

The letter X in the regression equation stands for age, while Y stands for fecundity and viability in equations for female and male trajectory, respectively. The regression coefficients were compared using non-parametric Kruskal–Wallis test of significance

absence of synchronization among the ageing patterns of the two sexes which caused varying progeny output.

The lower progeny production in the other groups was associated with a visually observed lack of synchronization between the fecundity and viability trends and statistically strengthened through the significant differences in the regression coefficients of these two trends. In the less progeny producing groups, the differences amongst the regression coefficients were statistically significant indicating that the trends in daily oviposition and viability were not synchronized, as also visible in the graphs.

The present results of variation in progeny output were obtained due to asynchronization between male and female ageing; as female age is responsible for the fecundity and male age for the fertility in ladybirds (Mishra and Omkar 2004; Srivastava and Omkar 2004; Omkar and Pervez 2005).

Previous studies on ageing trajectories in this beetle reveal reduction in fecundity of female after the age of 35 days while reduction in male viability is witnessed at an early age of 30 days (Mishra and Omkar 2006). Since the decline in males occurs earlier, young males should be paired with old females so that they attain their optima together and age synchronously. The difference in ages at which decline starts is probably because of different stocks that were used.

The difference in ages of individuals constituting a pair may result in either (1) wastage of eggs due to reduced sperm supply due to mortality or ageing of older male mates, or (2) wastage of sperm due to lesser egg production in the older female mates. The first scenario will definitely result in loss of female fitness, as it is dependent on the number of progeny produced, while the second scenario should lead to loss of male fitness, as it is dependent on the number of progeny sired (Nilsson 2004). However, the second case is less likely because not much energy is expended on sperm production, while egg production is costly (Majerus 2003).

The lack of coincidence among male and female ageing physiology, which has been observed in the present study, is supported by reports on the gonadal maturation of the two sexes in insects (Nunney 1996; Reed and Beckage 1997; Yasuda and Dixon 2002), including ladybirds (Ceryngier et al. 1992; Isogai et al. 1990). The non-coincidence of gonadal optima in similar aged counterparts may possibly be a result of their differential rates of metabolism or senescence. This difference in sexual maturation as depicted through 50% mating incidences has also been reported in *A. bipunctata* (Hemptinne et al. 2001), *C. septempunctata* (Srivastava and Omkar 2004) and pale morph of *P. dissecta* (Omkar and Pervez 2005). However, this can be conclusively confirmed only through detailed physiological studies on ladybirds.

The reduced fertility of eggs sired by older males lends support to the Hansen and Price (1995) model, which predicts that females should actively discriminate against older males because of the higher

deleterious mutations in their genome. Reduced progeny output as a result of high age difference (pairing with older male) in the present study may be ascribed to the senescence. Theoretically, in view of the loss of sperm discussed above, males should also avoid mating with older females. This hesitance of the younger females of *P. dissecta* to mate with older or very young males has been demonstrated in another study conducted by the authors (Omkar and Geetanjali Mishra, unpublished data). The older males were found to be actively spurned by the younger females. The younger males were also found to be reluctant in mating with older or middle aged females in the same study. The number of matings can also affect progeny output, as has been demonstrated in a number of studies (Omkar 2004; Omkar and Srivastava 2002). Thus, this age based behavior in mating could also be responsible for the lesser progeny output in the age groups in which either of the partners was much older than the other one. Another reason for the change in mating behavior could be that the alkanes involved in mate recognition (Hemptinne and Dixon 2000) may be reduced due to age or copulation, as in *Aedes aegypti* and *Anopheles gambiae* sensu stricto (Polerstock et al. 2002). Our unpublished data also reveal that offspring of pairs of young males with young females had the highest fitness, while those in which two older adults were paired had lowest fitness, thus providing an evolutionary reasons for restriction in progeny output (Omkar and Geetanjali Mishra, unpublished data).

Fecundity as well as viability are both known to be affected by mating frequencies in *P. dissecta* (Omkar et al. 2006). It is possible that the mating frequencies might differ in the various age differences studied in the present work. However, the effect of mating frequencies on fecundity and viability in *P. dissecta* extends only up to 12.95 and 11.25 matings, respectively (Omkar et al. 2006). These number of matings are very easily achieved in this ladybird as it copulates prolifically, with usually one prolonged mating per day (Omkar and Pervez 2005). In view of this, achieving the optimal number of matings in all setups does not seem to be a very difficult scenario. Thus, the effect of mating frequencies is not likely to be very prominent in this ladybeetle though it may hold true in case of insects with infrequent or less frequent matings.

The highlights of the study are: (1) age differences were studied for the first time in insects as a way to optimize age between the mates for the maximization of reproductive output, (2) Groups including pairs in which females were 5–10 days older than males resulted in maximum egg as well as progeny outputs when the pairing was at an young age, and (3) progeny output in pairs with various age differences is a result synchronization or the lack of it amongst ageing trends of both sexes.

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Author Biographies

Dr. Omkar and his research group works on aphidophagous ladybird beetles at the University of Lucknow. His interests lie in rhythmicity, reproductive biology, ageing, behavioral ecology, sexual selection, prey–predator and predator–predator interactions (dealing with cannibalism and intraguild predation along with the factors involved), especially amongst ladybirds. Of special interest is the identification of means of improving

biocontrol efficacy of ladybirds, especially aphidophagous ones.

Dr. Geetanjali Mishra —This research is a part of Ph.D. thesis of Dr. Geetanjali Mishra, who has been studying the effect of various factors, viz. prey species, gravity, light, rhythmicity, and ageing on the reproduction of a ladybird beetle, *Propylea dissecta* under the guidance of Dr. Omkar.