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The influence of age on reproductive performance of the predatory ladybird beetle, *Propylea dissecta*

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Abstract

The influence of age on reproductive performance of an aphidophagous ladybird beetle, *Propylea dissecta* was examined using male and female beetles of varying ages (1-30 days) after a single mating stimulus. All the intermediate (10 to 20 days old) and old (30 days old) age females mated with all intermediate and old age males, while only a fraction (0.29%) of younger females, 1 to 5 days old, mated with males of similar or older age. The willingness to mate was male age dependent. It increased sigmoidally with increase in adult age. Adult males were more willing to mate with females irrespective of age. Mating duration was longest amongst older adults (30 day-old males and 20 day-old females). Male age did not contribute to shaping the fecundity of the female ladybird. Fecundity was female age dependent and it increased with age up to 20 days and thereafter decreased. 20 day-old females were most fecund producing 867 eggs after a single mating. Progeny production was male age dependent and eggs sired by 20-30 day-old males had significantly higher viability than those sired by younger males. Prolonged mating increased fecundity and egg viability. The results reveal that males of intermediate age were better mates. This information may improve our understanding of the effect of aging on reproduction in ladybirds and may help mass-multiplication of the ladybird beetles using adults of optimal age.

Keywords: age, mating duration, fecundity, egg viability, aphid, *Aphis gossypii*

Introduction

The age of mating individuals is apparently a key factor in reproduction with effects on their sexual performance and progeny production. It is widely held that females should prefer to mate with older males in species where males provide only sperm to females, because viability selection leads to older males of higher genotype quality than younger males (Trivers, 1972; Manning, 1985; Anderson, 1994). In support of this hypothesis, a simulation model revealed a strong preference for older males under different eco-conditions (Kokko and Lindstrom, 1996). Several empirical studies have suggested that females do indeed prefer to mate with older males for their qualitative and quantitative progeny production (Zuk, 1988; Manning, 1989; Simmons and Zuk, 1992; Simmons, 1995). However, some have argued that males of young and intermediate ages are better mates, as they have the highest breeding value for fitness and are less prone to deleterious mutations (Hansen and Price, 1995; Beck and Powell, 2000).

Mating duration appears to influence fecundity and egg viability. In many insects, males mated for prolonged durations produce large ejaculates containing nutrients that are used by females for reproduction and somatic maintenance (Eberhard, 1996; Vahed, 1998). Thus, females obtaining larger ejaculates utilize these nutrients to lay more eggs and this operates to direct natural selection for mates that produce large ejaculates. That is, fecundity function may be linked with male age or status (Savalli and Fox, 1998; 1999). The role of age in a mating system, though theoretically and empirically assessed in other insects for a better understanding of its evolutionary significance, has been meagerly studied in predatory ladybirds (Coleoptera: Coccinellidae), the potential predators of phytophagous insect pests (Hodek and Honek, 1996; Omkar and Pervez, 2003a). As such, it was a major determinant in shaping the fecundity functions of aphidophagous ladybirds (Kindlmann *et al*, 2001; Omkar and Pervez, 2002; Dixon and Agarwala, 2002). Age-related mating incidence has revealed protogyny in the two-spotted ladybird, *Adalia bipunctata* L, (Hemptinne *et al.,* 2001), but protandry in a different ladybird, *Propylea dissecta* (Mulsant) (Omkar and Pervez, unpublished data). Information on how age influences mating behavior and reproduction in predaceous ladybirds may supplement our knowledge for their optimal rearing, and is thus of pragmatic relevance (Hodek and Ceryngier, 2000).

Considering the above evidence we tested the hypothesis that older males can be the better mates and attempted to provide answers to the following questions. Are older males more willing to mate? Is mating duration dependent on the age of mating partners? Does age have a regulatory role in reproductive performance of

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females? Does paternal age contribute to fecundity and progeny production? Does prolonged mating affect quantitative progeny production? Are older males better mates?

To seek answers to these questions and to evaluate age as a variant factor, experiments were designed to determine its influence on reproductive performance of an aphidophagous ladybird, *P. dissecta.* This is an Oriental ladybird beetle (Omkar and Pervez, 2000a) with high plasticity and can easily withstand the stress of prey deprivation by switching to other alternative foods (Omkar and Pervez, 2003b). It has been reported as an incidental predator of the coconut caterpillar, *Opsinia arenosella* (Pillai and Nair, 1986) and the aphids, *Aphis affinis* and *Myzus persicae* (Singh and Bali, 1993). But its over-abundance in aphid colonies of *Aphis gossypii* Glover infesting *Lagenaria vulgaris* Seringe in North India, as well as laboratory experiments, reveal it to be a potential biocontrol agent of this aphid (Pervez, 2002; Pervez and Omkar, 2004). It is polymorphic, with typical, intermediate and pale forms (R.G. Booth, personal communication) with the latter being more abundant in the agroecosystems around Lucknow, India. The relative abundance (> 60% of the ladybird population) and predatory efficiency of the pale morph was largely responsible for its selection as an experimental model for the present study.

Materials and Methods

Stock maintenance

Adults of the pale morph of *P. dissecta* were collected from agricultural fields in the suburbs of Lucknow, India and brought to the laboratory to establish stock cultures. For the stock, groups of 20 adult beetles (sex-ratio 1:1) were kept in glass jars (15.0 x 10.0 cm) containing moist filter paper for adults to oviposit at 27 ± 1° C, 65 ±5 % R.H. and LD 14: 10 h photoperiod. The jars were covered with fine muslin fastened with rubber bands. Preliminary experiments revealed that females significantly prefer to lay eggs on filter paper (Pervez, 2002). The beetles were fed daily on an *ad libitum* supply of *A. gossypii*-infested leaves of *L. vulgaris*. Eggs were collected from the filter paper and reared individually from egg hatch to adult emergence in glass beakers (8.0 x 11.0 cm) with a daily *ad libitum* supply of *A. gossypii*. The emerged adults were sexed on the basis of presence of black and white patches on their heads and pronota (Omkar and Pervez, 2000b) and kept separately in Petri dishes (9.0 x 1.5cm) containing *A. gossypii* on the host plant. Thus, both unmated male and female ladybirds of known ages (*i.e.* newly emerged, 1, 2, 3, 4, 5, 10, 20 and 30 days old) were kept separately.

Experimental design

A newly emerged unmated male was paired with a newly emerged virgin female in a Petri dish at 10:00 AM. They were observed continuously for 30 min and thereafter every half an hour until 6:00 PM (the time at which they were separated). If mating occurred, the behavior of the two ladybirds and the mating duration was recorded. After termination of mating, the female was carefully observed for 30 min to record the ejection of spermatophore or any jelly like material. The female was isolated from the male and kept for further observations on pre-oviposition, oviposition, and post oviposition periods, fecundity, and percent egg viability (n=10). Only a single mating was allowed. Similarly, newly emerged males were paired with 1, 2, 3, 4, 5, 10, 20 and 30 day-old virgin females (n=10). The mated females were reared separately in Petri dishes with prey and space provided as described above, with daily replenishment of prey. Eggs laid by females were counted and transferred to separate Petri dishes to avoid cannibalism. The experiment was repeated, using 1, 2, 3, 4, 5, 10, 20 and 30 day-old unmated males with the virgin females of varying ages (n=10).

Statistical Analysis

Data on mating duration, pre-oviposition, oviposition, and post oviposition periods, fecundity, and percent egg viability in females of varying ages crossed with males of varying ages were recorded and subjected to a 4 x 4 factorial ANOVA followed by Bonferroni's Post Hoc Test using the statistical software SPSS on a personal computer. Relationships between age and (i.) mating duration, (ii.) fecundity, and (iii.) egg viability were estimated using non-linear regression analysis using a statistical software MINITAB.

The willingness of the two sexes to mate was determined using following formula:

$$W = N_1 \times 100 / N$$

Where, W= willingness (%) of a partner (male or female) to mate, N_1 = number of individuals of same age that mated with counterparts of varying ages, and N = number of individuals of same age that were paired with counterparts of varying ages (n = 90, as there were 9 sets of varying ages in 10 replicates). The data on willingness of each sex to mate were subjected to arcsine square root transformation and fitted with the adult age using a statistical software MINITAB.

Results

Mating behavior

The males of *P. dissecta* started mating when 3 days-old, while females of all ages (newly emerged to 30 days-old) mated with the older males (10 to 30 days-old). Younger females (5 days-old pooled), though reluctant, were forcefully mated by older males. Older females (10 to 30 days-old) that became static were palpated by the younger males, prior to mating. Older adults (10 to 30 days-old) showed 100% mating with each other, while only a fraction (0.29% of males and 0.29% of females) of younger adults mated either with similar or older individuals of the opposite sex. The data on mating duration and reproductive attributes of younger (1 to 5 day-old) adults were pooled prior to statistical analysis to remove the statistical problem of varying degrees of freedom. The females ejected no spermatophore or jelly like material after mating.

Are older males more willing to mate?

There was a sigmoidal increase in willingness to mate with increase in male age (Figure-1a). Males that were 2 days old or younger were unwilling (0%) to mate, while those over 10 days old were more willing (81.11 to 83.33 %). A similar sigmoidal increase in willingness to mate was also observed for females with 51.11 to 52.22% of the older females (10 to 30 days-old) were willing to mate (Figure 1b).

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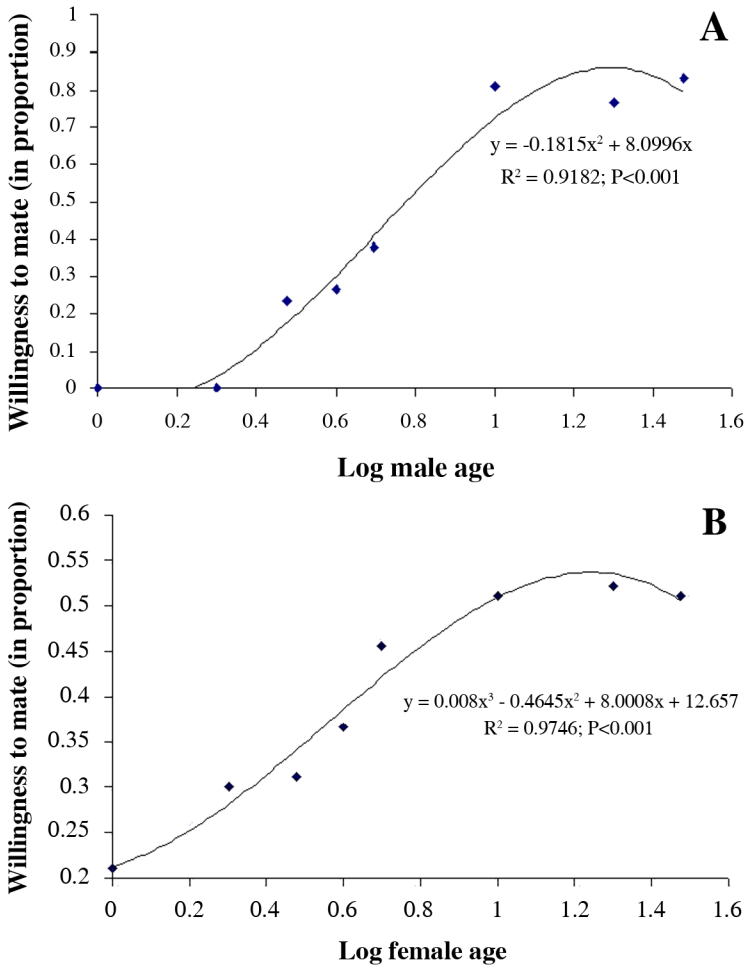

Figure 1. A. Effect of male age on the mating willingness of *Propylea dissecta*. B. Effect of female age on the mating willingness of *Propylea dissecta*.

Is mating duration dependent on the age of mating partners?

Mating duration was dependent on the age of mating partners and it varied significantly with increase in both male and female ages (Table-1). The 4 X 4 factorial ANOVA used to test significance within and between the variables, revealed a significant main effect of mating duration (F (3, 108) = 37.41; P < 0.001) and age (F (3, 36) = 32.59; P < 0.001). The results, however, did not reveal a significant interaction between age and mating duration (F (9, 108) = 1.52; P > 0.05). Mating duration followed a similar pathway when regressed with both male and female ages (Figures 2, 3). The best-fit lines revealed that maximum mating duration occurred 26.0 and 21.0 days after emergence in males and females, respectively.

Does age have a regulating role in reproductive performance of female?

Table-1 shows that mating duration, fecundity, reproductive and non-reproductive periods were significantly affected by female age. Factorial ANOVA revealed a significant main effect of pre-oviposition period (F (3, 108) = 4481.62; P < 0.001) and age (F (3, 36) = 2.75; P < 0.05). The interaction between age and pre-oviposition period was found to be statistically significant (F (9, 108) = 2.08; P < 0.05). A significant main effect of oviposition period, (F (3, 108) = 20.51; P < 0.001) and age (F (3, 36) = 46.54; P<0.001) was found. There was a significant interaction between age and oviposition period (F (9, 108) = 3.12; P<0.01). A significant main effect of post-oviposition period (F (3, 108) = 233.56; P < 0.001) and age (F (3, 36) = 6.68; P < 0.001) was found. The interaction between age and post-oviposition period, however, was not statistically significant (F (9, 108) = 1.58; P > 0.05). There was a significant main effect of fecundity (F (3, 108) = 19.30; P <

Table 1. Biological attributes of females of varying ages of *P. dissecta*, when once mated with males of varying ages (n=10).

Male age when mated with female		Mating Duration (in min)	Pre-oviposition period (in days)	Oviposition period (in days)	Fecundity (in eggs)	Per cent Viability	Post Oviposition Period (in days)
1-5d female (pooled)	1-5d male	165.0±18.17	8.20±0.25	22.10±2.05	127.30±7.82	46.30±2.38	52.50±2.79
	10d male	169.50±5.33	8.30± 0.33	26.74±2.44	168.60±13.57	63.89±2.40	51.50±3.66
	20d male	198.10±6.18	9.00± 0.52	42.00±1.79	219.10±9.04	71.53±1.81	45.10±1.78
	30d male	209.10±4.72	8.60± 0.45	50.60±5.74	257.20±39.63	72.70±2.24	42.60±6.14
10d female	1-5d male	174.40±8.06	12.50±0.27	34.10±4.39	202.50±23.60	50.63±1.48	30.30±2.41
	10d male	187.70±8.74	12.60± 0.27	46.60± 5.41	278.30± 35.65	66.79±1.56	23.70± 4.10
	20d male	239.00±14.23	11.80± 0.13	86.90± 3.99	361.10±21.48	71.82±3.18	16.60± 2.45
	30d male	271.80± 6.98	11.60± 0.16	69.40± 4.64	328.60±19.73	77.18±1.42	18.60± 2.02
20d female	1-5d male	230.5±10.84	21.10±0.35	39.10±3.13	207.20±22.17	57.60±2.87	11.20±1.12
	10d male	257.90± 12.98	21.30±0.45	56.50± 11.14	389.80± 71.95	72.51± 3.14	5.80± 0.59
	20d male	302.00± 31.06	21.20±0.13	59.10± 4.67	405.60±25.12	76.89± 1.46	6.40± 0.85
	30d male	364.80± 25.85	20.70±0.15	84.60± 6.59	373.80± 17.66	81.96± 1.32	8.50± 0.37
30d female	1-5d male	175.6±18.16	31.60±0.22	38.40±4.69	175.30±12.74	51.21±2.70	7.0±0.62
	10d male	223.3±12.31	30.8± 0.20	50.00± 5.91	318.30± 23.05	73.32± 0.75	4.80±0.68
	20d male	248.40±16.75	30.40± 0.16	67.00± 1.94	362.80± 21.97	76.67±0.81	6.80±0.88
	30d male	290.60±9.90	30.5± 0.17	63.50± 2.32	334.70± 41.59	79.46±1.03	5.60±0.56

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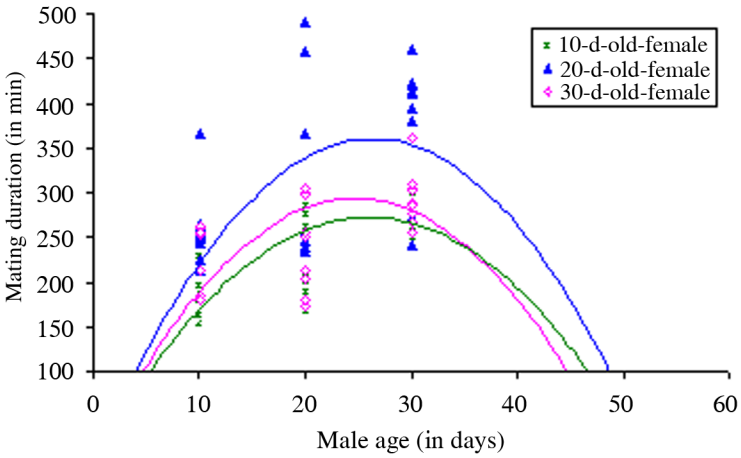

Figure 2. Effect of male age on mating duration of *Propylea dissecta*. 10 day-old males (green; Y = 118 + 7.91 x – 0.093 x^2; r^2 = 0.549; P < 0.001). 20 day-old males (blue; Y = 233 + 1.60 x – 0.094 x^2; r^2 0.632; P < 0.001). 30 day-old males (pink; Y = 215 – 0.05 x + 0.836 x^2; r^2 = 0.792; P < 0.001). Best fit lines.

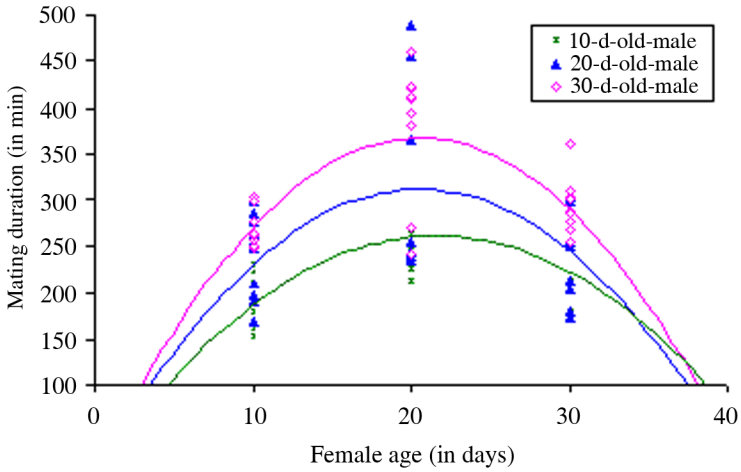

Figure 3. Effect of female age on mating duration of *Propylea dissecta*. 10 day-old males (green; Y = 12.7 + 22.7 x – 0.542 x^2; r^2 = 0.623; P < 0.001). 20 day-old males (blue; Y = 59.4 + 23.8 x – 0.583 x^2; r^2 0.51; P < 0.001). 30 day-old males (pink; Y = 11.6 + 34.4 x – 0.836 x^2; r^2 = 0.75; P < 0.001). Best fit lines.

0.001) and age (F (3, 36) = 20.60; P < 0.001). The results, however, did not show a significant interaction between age and fecundity (F (9, 108) = 1.07; P > 0.05). The post-hoc analyses are presented in Tables 2 and 3.

Females that mated at a younger age had a relatively shorter pre-oviposition period and a longer post oviposition period than those that mated at an older age (Table 1). Similar trends of mating duration (Fig. 3) and fecundity (Fig. 4) were obtained with female age. The regression analysis revealed that female age does regulate reproductive performance particularly in terms of mating duration and fecundity. Both of these parameters increased with female age, peaked at 20 days and decreased with further aging. The maximum individual fecundity (867 eggs with an oviposition period of 106 days) occurred when 20 day-old females mated with 10 day-old males.

Does paternal age contribute to fecundity and progeny production?

Male age did not affect fecundity of females, however it did contribute to progeny production as the eggs sired by the 30 day-old males were most viable (Table 1). The 4 x 4 factorial ANOVA revealed that the main effects of egg viability (F (3, 108) = 18.18; P < 0.001) and age (F (3, 36) = 93.70; P < 0.001) were statistically significant. The interaction, however, was insignificant between them (F (9, 108) = 1.78; P = 0.08).

Do prolonged matings affect quantitative progeny production?

Figures 2 to 5 show that the effects of age on mating duration are similar to the effects of aging on fecundity and percent

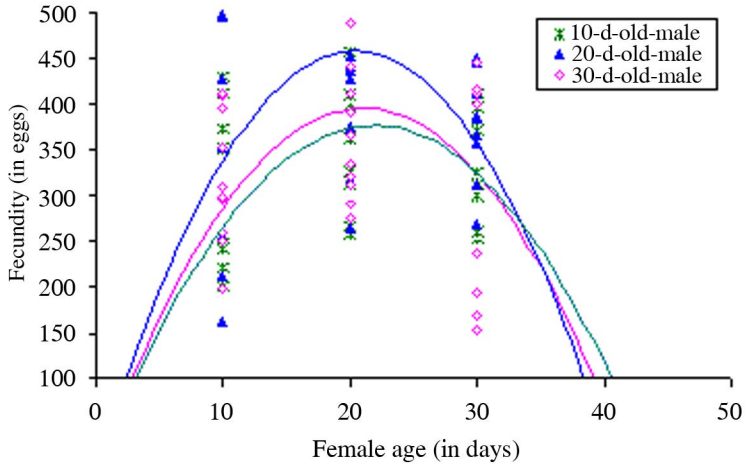

Figure 4. Effect of female age on fecundity of *Propylea dissecta*. 10 day-old males (green; Y = 80.0 + 25.6 x – 0.576 x^2; r^2 = 0.54; P < 0.001). 20 day-old males (blue; Y = 326 + 8.7 x – 0.238 x^2; r^2 0.64; P < 0.001). 30 day-old males (pink; Y = 201 + 15.3 x – 0.363 x^2; r^2 = 0.75; P < 0.001). Best fit lines.

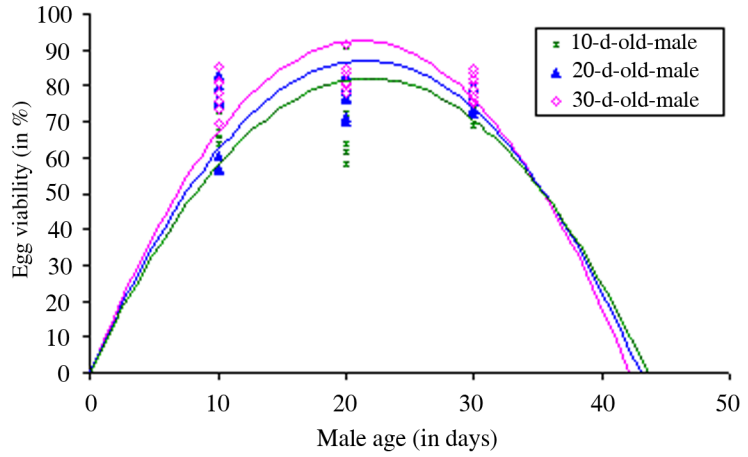

Figure 5. Effect of male age on percent egg viability of *Propylea dissecta*. 10 day-old males (green; Y = 52.2 + 1.31 x – 0.25 x^2; r^2 = 0.72; P < 0.001). 20 day-old males (blue; Y = 61.5 + 1.3 x – 0.027 x^2; r^2 0.65; P < 0.001). 30 day-old males (pink; Y = 65.1 + 1.57 x – 0.367 x^2; r^2 = 0.64; P < 0.001). Best fit lines.

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Table 2. Paired sample t-test of mating duration, pre-oviposition period and oviposition period of P. dissecta followed by Bonferroni Post-Hoc analysis.

Paired Sample t-test			Bonferroni Post-Hoc Analysis
Pairs	Mean Differences	t-value	Mean Differences
MD5 – MD10	-32.80± 6.43	-5.10***	-23.22±10.62
MD5 – MD20	-103.38±12.15	-8.51***	-60.50±10.62***
MD5 – MD30	-49.05±8.63	-5.69***	-97.70±10.62***
MD10 – MD20	-70.58±9.98	-7.07***	-37.28±10.62**
MD10 – MD30	-16.25±8.76	-1.86	-74.47±10.62***
MD20 – MD30	54.33±13.49	4.03**	-37.20±10.62**
PE5 – PE10	-3.60±0.23	-15.74**	0.10±0.19
PE5 – PE20	-12.55±0.27	-47.28***	0.25±0.19
PE5 – PE30	-22.30±0.25	-87.90***	0.50±0.19
PE10 – PE20	-8.95±0.18	-49.07***	0.15±0.19
PE10 – PE30	-18.70±0.16	-119.19***	0.40±0.19
PE20 – PE30	-9.75±0.21	-46.87***	0.25±0.19
OV5 – OV10	-23.90±3.54	-6.75**	-11.53±3.30**
OV5 – OV20	-24.48±4.08	-6.01**	-30.33±3.30***
OV5 – OV30	-19.38±2.82	-6.88**	-33.60±3.30***
OV10 – OV20	-0.58±5.04	-0.11	-18.80±3.30**
OV10 – OV30	4.52±3.15	1.44	-22.07±3.30***
OV20 – OV30	5.10±4.24	1.2	-3.27±3.30

Note : MDn = mating duration (in min.), Pen = pre-oviposition period (in days), OVn = oviposition period (in days). * P < 0.05, ** P < 0.01, and *** P<0.001; df = 39

Table 3. Paired sample t-test of Post-Oviposition Period, Fecundity and Egg Viability of *P. dissecta* followed by Bonferroni Post-Hoc Analysis.

Paired Sample t-test			Bonferroni Post-Hoc Analysis
Pairs	Mean Differences	t-value	Mean Differences
PO5 – PO10	25.62±2.49	10.29**	3.80±1.68
PO5 – PO20	39.95±2.04	19.58***	6.52±1.68**
PO5 – PO30	41.88±1.99	21.01***	6.43±1.68**
PO10 – PO20	14.33±1.57	9.11**	2.72±1.68
PO10 – PO30	16.25±1.70	9.57**	2.62±1.68
PO20 – PO30	1.92±0.58	3.33*	-0.10±1.68
FU5 – FU10	-99.57±15.67	-6.36**	-110.67±22.48***
FU5 – FU20	-151.05±24.25	-6.23**	-159.08±22.48***
FU5 – FU30	-104.72±16.20	-6.47**	-145.50±22.48***
FU10 – FU20	-51.48±26.11	-1.97	-48.40±22.48
FU10 – FU30	-5.15±17.11	-0.3	-34.82±22.48
FU20 – FU30	46.33±21.35	2.17*	13.58±22.48
EV5 – EV10	-2.26±1.41	-1.6	-18.44±1.68***
EV5 – EV20	-7.19±1.38	-5.21**	-24.29±1.68***
EV5 – EV30	-8.90±1.42	-6.25**	-24.10±1.68***
EV10 – EV20	-4.93±1.41	-3.50**	-5.86±1.68**
EV10 – EV30	-6.64±1.21	-5.51**	-5.67±1.68**
EV20 – EV30	-1.71±1.65	-1.03	0.19±1.68

POn = Post-Oviposition period (in days), FUn = Fecundity (in eggs), EVn = Egg Viability (in percent). * P < 0.05, ** P < 0.01, and *** P<0.001; df = 39

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egg-viability in the sense that they peak at similar times. Mating duration also has a significant positive correlation with fecundity (r=0.416; P<0.05) and egg-viability (r=0.454; P<0.05), which reveals that increase in mating duration increases the progeny production. Thus, it can be inferred that prolonged mating affects quantitative progeny production.

Are older males better mates?

Although 20-30 day-old males showed the best reproductive performance in terms of mating duration and percent egg viability (Tables 1, 3), best-fit lines suggest that a decrease in mating duration and viability of eggs may occur in males aged over 30 days (Figs. 3 and 5).

Discussion

These results clearly indicate that age does have a significant effect on the reproductive attributes of both male and female ladybirds. Willingness to mate was found to be dependent on adult age and increased with aging. The minimum age at which males mated was 3 days after emergence, during which time the elytra harden (Omkar and Srivastava, 2002) and the gonads mature (Ceryngier et al., 1992). The males were more responsive towards older females, possibly due to the high mating willingness of latter, who became static when palpated, which allows males to mate with them. Gradual aging in males enhanced their willingness to mate, as older males were most willing to mate irrespective of the females' age. They forcefully mated with newly emerged females with unhardened elytra and incomplete pigmentation revealing male dominance in mating, at least under laboratory conditions. Our results disagree with earlier reports of the unresponsiveness of males towards newly emerged females, owing to their lack of pigmentation and unhardened elytra (Obata, 1988a; Majerus, 1994; Hodek and Honek, 1996). The physiological status of male is supposed to have a driving role in the sexual activity of ladybirds (Omkar and Srivastava, 2002).

Mating duration was found to be dependent on the age of mating partners, and adults of intermediate age mated longer than younger ones. The reasons for the longer mating duration are unclear. However, it is possibly due to the increased intensity of the older male's urge to mate or to prolonged or multiple sperm transfer due to prolonged mate deprivation. In an aphidophagous two-spot ladybird, *Adalia bipunctata*, mating is prolonged due to multiple ejaculations, *i.e.* sperm transfer occurs two or three times in a single mating (Majerus, 1999). The prolonged or multiple ejaculations appear to increase progeny production (Majerus, 1999). Relatively high mating duration in ladybird, *Propylea japonica* was reported, when they mated only once as compared to other ladybirds, *viz. Harmonia axyridis, Coccinella septempunctata* and *Cheilomenes sexmaculata* (Obata and Johki, 1991).

A significant influence of age was found on reproductive attributes of females suggesting that age does have a regulatory role in their reproductive performance. The pre-ovipositional period increased with increase in female age, which suggests that oviposition is mating dependent in *P. dissecta* and that virgin females cannot lay eggs. However, in other insects, *i.e.* in apple moth, *Epiphyas postvittana*, virgin females can lay unfertile eggs before mating (Foster and Howard, 1999). Fecundity was significantly dependent on female age with 20 day-old mated female exhibiting maximum fecundity. The present study supports a relatively high fecundity after single mating with a female laying a maximum of 867 eggs, as compared to other studies on *C. sexmaculata* (Bind, 1998), *C. transversalis* (James, 2001) and *C. septempunctata* (Omkar and Srivastava, 2002). The increased fecundity in females of intermediate age may be due to higher number of mature ova than are present in young females, as also suggested by Obata (1988b). Twenty day-old females may be optimal for studies pertaining to reproduction in *P. dissecta* and for optimal egg production.

Females that mated at a young age (1 to 4 days-old) oviposited late (*i.e.* after 4 to 7.5 days), which may be attributed to the probable immature gonads that had taken some time to mature ((Hemptinne et al., 2001). The resultant viable eggs laid by these females revealed that the sperm stored in spermathecae since mating fertilized the ova once females became sexually mature. It is possible that immature females store sperm for progeny production in absence of males (Hemptinne *et al.,* 2001). This may be a part of her reproductive strategy to secure her progeny. Older females oviposited just few hours after mating, which probably indicates the presence of mature ova in their ovaries.

Paternal (male) age has a seemingly insignificant role in shaping the fecundity of females, with no apparent effect of the male-ejaculate. During the insemination process in ladybirds, the sperm are transferred either directly or via a sac-like spermatophore, which is usually ejected by the female after copulation (Obata and Johki, 1991; Omkar and Srivastava, 2002). The failure of female *P. dissecta* to eject spermatophores suggests that sperm are directly transferred (Obata and Johki, 1991; Chapman, 1998). Other nutrients are apparently not transferred in *P. dissecta*, which, in some species, are necessary for female fitness, somatic maintenance and egg production. However, in those ladybirds where sperm transfer is via a spermatophore other essential nutrients needed to increase female fitness may be transferred. The present study suggests no effect of male age on female fitness, and opens avenues of further research on ladybirds where sperm are transferred via spermatophore.

Although paternal age does not affect fecundity in females, it does affect the viability of eggs, as the eggs sired by 20-30 day-old males were more viable than those sired by younger males. This may be due to the increased transfer of sperm by the 20-30 day-old males. Our results are at odds with those of Kokko and Lindstrom (1996) who suggested that females mating with younger males would have optimal quantitative progeny, but support Hansen and Price (1995) and Beck and Powell (2000) that females should prefer males of intermediate age. Moreover, it is likely that older individuals have better-quality genes to pass on to their offspring, as they themselves obviously have high survival rates (Promislow, 2003).

Trends of mating duration were found similar to those of fecundity and egg viability with maximum mating duration coinciding with high fecundity and egg viability. This suggests that prolonged matings may result in deposition of increased quantity of sperm, which are stored in the spermathecae by the females to fertilize the ova during non-mating conditions and may result in increased lifetime fertility. Our results, although not conclusive,

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suggest that egg production is female age dependent, while progeny production is male age dependent. Females that mated at a younger age had a relatively longer post-oviposition period, which may indicate that cessation of oviposition is a temporary event. Opportunity for multiple matings in the post oviposition period by females subjected to single mating may retain their reproductive performance, but this needs further studies. Thus, owing to the predicted estimates, we can conclude that adults of intermediate age are best mates and can produce best reproductive performance.

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