Effect of age on reproductive attributes of an aphidophagous ladybird, *Cheilomenes sexmaculata*

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Abstract The effect of both male and female age was investigated on certain reproductive attributes, *viz*. mating incidence, mating duration, fecundity, percent egg viability, ratio of reproductive and non-reproductive periods and reproductive rate, of an aphidophagous ladybird, *Cheilomenes sexmaculata* (Fabricius). Females started mating at the age of 8 hours post-emergence (PE) and males at the age of 2 days PE. Mating in the laboratory was a male-dominated phenomenon. The mating duration and reproductive rate of 10-day-old females when mated with males of varying ages increased up to the male age of 60 days, and thereafter decreased, whereas, fecundity, egg viability and ratio of reproductive and non-reproductive periods increased up to the male age of 50 days, and thereafter declined. However, when females of varying ages were mated with 10-day-old males, fecundity and reproductive rate increased up to 40 days of female age, respectively, then decreased. The ratio of reproductive and non-reproductive periods increased with increasing age of females. Mating age for optimal reproductive output was 10−50-day-old males and NE to 40-day-old females. Reproductive cessation in males was recorded after 50 days PE, whereas in females at the age of 40 days PE. Higher mating durations lead to elevated reproductive rates. Delay in the reproductive phase was positively correlated with longevity. The results of this study may aid mass multiplication of this ladybird by identifying and promoting usage of adults of optimal age. Our results also enhance our understanding of the effect of age on reproductive attributes in ladybirds.

Key words age, *Cheilomenes sexmaculata*, egg viability, fecundity, ladybird, longevity, protogyny, reproduction, reproductive rate

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Introduction

Age plays a major role in determining various life-history attributes of organisms. The physiology of these organisms is under constant stress during their struggle against fluctuating environmental conditions. As a part of their struggle they attempt to achieve a balance between early and late age fitness for successful survival, which is expressed as age-specific variations in various life history attributes. This process eventually leads to a state of deterioration with increase in age, that is, senescence leading ultimately to death (Mangel, 2002). Senescence has recently been expressed as a naturally selected stress resistance-dependent phenomenon which allows individuals to resist the germ-cell enforced death sentence, at least for some time (Heinninger, 2002).

Among insects, the effect of age is well studied in terms of mate choice by females with emphasis on evolutionary consequences. According to good genes theory and/or the viability indicator model, the females prefer older males of higher genotype quality in species where males provide only sperm to females, because they have proved their superiority in terms of longevity (Manning, 1985; Kokko & Lindstrom, 1996). Hansen and Price's (1995) trade-off model disagrees with the above and suggests that pairing

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with older males can lead to reduction in progeny output. This has been further supported in later years with the interpretation that young-to-intermediate aged males should give best results (Beck & Powell, 2000; Jones *et al.*, 2000).

Reproduction in organisms, including insects, is a costly process (Omkar & Mishra, 2005), which involves an obligate trade-off with other life-history traits (Mishra & Omkar, 2006). The near universality of this finding suggests that the reproductive activity is a major pacemaker of senescence and death (Rose, 1984; Sgro & Partridge, 1999). These findings were further supported by the fact that reproductive diapause in a variety of adult insects and delay of sexual maturation or reproductive phase in *Nereis* and *Coenorhabditis elegans* slows the process of senescence, thus increasing the longevity (Johnson *et al.*, 1984; Tartar & Yin, 2001). These findings indicate that longevity requires investments in somatic maintenance and repair that must compete against investments in growth, reproduction and fitness-enhancing activities.

Predaceous ladybirds (Coleoptera: Coccinellidae) are potential biocontrol agents for numerous phytophagous insect and acarine pests. Previous age-related studies have largely concentrated on age-specific fecundity and factors affecting it (Dixon & Agarwala, 2002; Omkar & Pervez, 2002). However, recent research reveals that the reproductive performances of *Coccinella septempunctata* Linnaeus and *Propylea dissecta* (Mulsant) vary with age (Srivastava & Omkar, 2004; Pervez *et al.*, 2004; Omkar & Pervez, 2005). The male age affects percent egg viability, while female age affects fecundity in aphidophagous ladybirds (Mishra & Omkar, 2004).

In light of the above information an attempt was made to evaluate the effects of age at mating on various reproductive attributes, *viz.* mating incidences, fecundity, percent egg viability, ratio of reproductive and non-reproductive periods and reproductive rate in a ladybird, *Cheilomenes sexmaculata* (Fabricius). Additionally, the study also attempted to define relationships between mating duration and reproductive rate, and longevity and delay in reproduction in *C. sexmaculata*. These two aspects, to the best of our knowledge, have not been previously studied in aphidophagous ladybirds.

Cheilomenes sexmaculata is a generalist predatory ladybird, common in Asia (Tao & Chiu, 1971; Omkar & Bind, 1993). In the Indian subcontinent it preferentially feeds on aphid, *Aphis craccivora* Koch leading to high growth, development and reproductive output (Omkar & Bind, 2004; Omkar *et al.*, 2004). Age-specific studies on this ladybird illustrated decreasing activity patterns with age (Dixon & Agarwala, 2002) and age-specific clutch size (Omkar *et al.*, 2004). However, elaborate studies dealing with effects of age on various life history traits are still meager per se in ladybirds. Knowledge on effects of age on reproductive attributes may prove to be useful in developing mass multiplication and use of ladybirds in pest management strategies, facilitating their augmentative field releases. Further, the results will help us to understand the basic biology and process of senescence in ladybirds.

Materials and methods

Stock culture

Twenty adult males and females of *C. sexmaculata* were collected from the colonies of aphid, *A. craccivora* infested on bean (*Dolichos lablab* Linnaeus) in the fields around Lucknow in November 2003 and brought to the laboratory. They were paired for mating and kept in an environmental test chamber (REMI Instruments, CH-6S; Mumbai) (25 ± 2°C, 60% ± 5% RH and 10L:14D) in Petri dishes (9.0 × 1.5 cm) containing *ad libitum* prey. Eggs laid were collected daily and the hatched instars reared till pupation in glass beakers (11.0 × 9.0 cm) on daily replenishment of prey. Beakers containing pupae were observed twice a day and newly emerged adults separated in Petri dishes (prey and abiotic conditions as above). The adults were sexed and separated according to their ages (post-emergence).

Effect of adult age on mating incidences

The newly emerged (NE, 8 hours old) adults of *C. sexmaculata* were kept separately in Petri dishes (space and prey as above). NE males were paired with NE, 1, 2, 4, 6, 8, and 10-day-old virgin females in Petri dishes separately one pair/dish at 1 000 h (*n* = 10). If mating occurred (occurrence of mating was ascertained by observing genital contact under WILD Binocular stereoscope at 16 × magnification), the behaviour of the mates and mating duration was recorded. Only single mating was allowed and females were isolated post-mating. Similarly 1, 2, 4, 6, 8, and 10-day-old males were also subjected to pairing with different aged virgin females and the mating incidences between unmated males and virgin females over the range of ages were determined (*n* = 10).

Effect of adult age on reproductive attributes

To examine the effect of male age on reproductive attributes, 10-day-old virgin females were mated singly with previously unmated males of varying ages (from NE to 110 days). Thus, the following combinations were made: (female age × male age: 10 × NE, 10 × 4, 10 × 10, 10 × 20, 10 × 30, 10 × 40, 10 × 50, 10 × 60, 10 ×

80, 10 × 100, 10 × 110) (*n* = 10) at above abiotic conditions. Similar sets were designed to evaluate the effect of female age, keeping male age constant (10-day-old) and varying female age (NE to 110). Females were isolated after single mating and reared singly on daily replenishment of *ad libitum* prey (as above) till their death (*n* = 10). In each combination, mating duration, fecundity, percent egg viability, pre-oviposition, oviposition and post-oviposition periods were recorded.

Data analysis

   The percentage of mating incidences at different ages of ladybirds was analyzed by chi-square (χ^2) goodness-of-fit test using the statistical software MINITAB on a personal computer. The cumulative mating incidences (CMI) were calculated as:

$$CMI = (TMI / Nc) \times 100,$$

where TMI is total mating incidences by an individual at a particular age with a mate of any age, and Nc is the total number of individuals used at that particular age.

   Percent mating incidences were plotted against age of individuals to demonstrate the age of sexual maturation. Ratio of reproductive and non-reproductive periods [oviposition period / (pre-oviposition period + post-oviposition period)] was calculated and transformed into $\log_{10}$ values. It gives a statistical measure of the proportion of a female's life span devoted to reproduction. Reproductive rate (fecundity / oviposition period) was also calculated.

   Data on mating duration, fecundity, percent egg viability, oviposition period, ratio of reproductive and non-reproductive periods and reproductive rate were subjected to one-way ANOVA followed by post hoc Tukey's test of significance. Relationship of age of both sexes with cumulative mating incidences, mating duration, fecundity, percent egg viability, $\log_{10}$ reproductive and non-reproductive periods ratio and reproductive rate were estimated using

non-linear regression analysis. Similar analysis was applied between mating duration and reproductive rate and longevity and pre-mating period (referred to as reproductive phase delay). All statistical analyses were performed using the statistical software MINITAB (2003) on a personal computer.

Results

Effect of adult age on mating incidence

   The mating incidence increased with increase in age of both adult male and female *C. sexmaculata* (Table 1). The adult male and female ladybirds started mating when they were 2 days old and newly emerged, that is, 8 hours old, respectively. Six to 10-day-old males were more successful in establishing mating (Table 1). Sixty-one percent of males were successful in establishing mating at the age of 2 days and this increased up to 100% at the age of 10 days. The willingness to mate increased significantly with increase in male age ($Y = 7.9 + 22.9 X - 1.43 X^2$; $r = 0.94$; $P < 0.001$; Fig. 1). Seventy-six percent of females mated at an early age of 8 hours and their receptivity increased with increase in age ($Y = 77.7 + 1.44 X - 0.026 X^2$; $r = 0.82$; $P < 0.001$; Fig. 1). The receptivity at each age in females was also dependent upon the age of mates. Even NE females were 100% receptive for 10-day-old males.

Effect of adult age on reproductive attributes

   Mating duration increased with increase in male age up to 60 days and thereafter decreased significantly ($F = 10.68$; df = 14,104; $P < 0.001$) with increasing male age ($Y = 72.2 + 0.674 X - 0.00942 X^2$; $r = 0.50$; $P < 0.05$). Mating duration also increased significantly with increase in female age ($F = 4.03$; df = 14,104; $P < 0.01$; $Y = 67.2 + 0.046$

Table 1 Mating incidences among males and females of *C. sexmaculata* of different age.

Male age (days)	Female age (days)							χ^2 test
	NE	1	2	4	6	8	10	
NE	0	0	0	0	0	0	0	—
1	0	0	0	0	0	0	0	—
2	50%	50%	70%	70%	60%	60%	70%	14.7
4	70%	80%	80%	80%	70%	80%	88.9%	16.4
6	80%	90%	80%	90%	90%	100%	100%	18.1
8	80%	90%	90%	80%	100%	100%	100%	18.3
10	100%	100%	100%	100%	100%	100%	100%	21.1
χ^2 test	11.7	12.5	12.5	13.8	12.3	13.6	12.3	

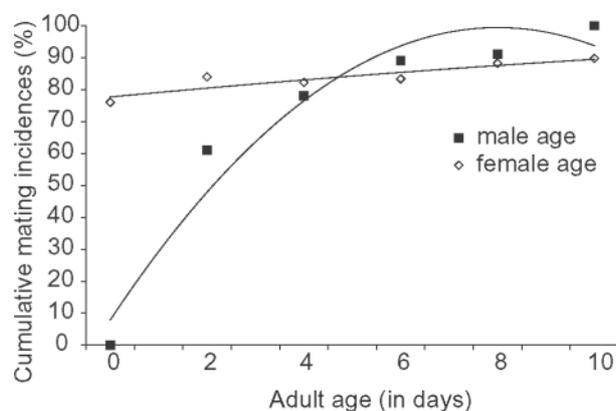NE = newly emerged (8-hour-old); Values are significant at $P < 0.01$.

Fig. 1 Effect of male and female ages on mating incidence in *C. sexmaculata* (Age of mated individual is 10 days).

$X + 0.00302 X^2$; $r = 0.27$; $P < 0.05$). The highest mating duration was recorded when 100-day-old females mated with 10-day-old males (142.5 ± 1.21 min) and lowest when 100-day-old males mated with 10-day-old female (28.25 ± 0.53 min).

Fecundity increased with increase in both male ($F = 111.57$; df = 14,104; $P < 0.001$) and female ($F = 64.63$; df = 14,104; $P < 0.001$) ages (up to 50 days of male age and 40 days of female age), which decreased on further increase in adult age and revealed significant trend lines when fitted against increasing male ($Y = 1190 + 1.9 X - 0.126 X^2$; $r = 0.73$; $P < 0.05$; Table 2) and female ($Y = 1347 - 1.99 X - 0.0965 X^2$; $r = 0.91$; $P < 0.001$; Table 3) ages. Fecundity was highest (1464.4 ± 2.18 eggs) when 40-day-old males

mated with 10-day-old females and lowest (42.8 ± 1.00 eggs) when 110-day-old males mated with 10-day-old females. Percent egg viability increased with increase in age of males up to 50 days ($F = 54.25$; df = 14,104; $P < 0.001$) and thereafter decreased with further increase in age ($Y = 108 - 1.00 X + 0.00086 X^2$; $r = 0.71$; $P < 0.1$; Table 2). However, it did not vary significantly with female age ($F = 0.72$; df = 14,104; N.S.; $Y = 73.5 + 0.432 X - 0.00288 X^2$; $r = 0.17$; $P > 0.05$; Table 3). Percent egg viability was highest (90.71% ± 0.13%) when 50-day-old females mated with 10-day-old males and lowest (11.90% ± 0.26%) when 110-day-old males mated with 10-day-old females. Oviposition period varied significantly with varying male ($F = 100.86$; df = 14,104; $P < 0.001$) and female ($F = 63.72$; df = 14,104; $P < 0.001$) ages. Post hoc analysis revealed prominent decrease in oviposition period after 50 days of male and 60 days of female age. The highest (55.25 ± 0.05 days) oviposition period was obtained when 30-day-old females mated with 10-day-old males and lowest (5.25 ± 0.01 days) when 110-day-old females mated with 10-day-old males.

The ratio of reproductive and non-reproductive periods increased up to the male age of 40 days, thereafter decreased significantly with increasing age ($F=13.65$; df = 14,104; $P < 0.001$; $Y = -0.392 + 0.0527 X - 0.000426 X^2$; $r = 0.47$; $P < 0.05$; Table 2). However, a steady increase was found with increasing female age ($F = 2.44$; df = 14,104; $P < 0.05$; $Y = 0.130 + 0.0100 X + 0.000004 X^2$; $r = 0.92$; $P < 0.001$; Table 3). The highest ratio (25.63 ± 0.53) of reproductive and non-reproductive periods was obtained when 40-day-old males mated with 10-day-old females

Table 2 Reproductive attributes of 10-day-old female *C. sexmaculata* when mated singly with males of varying age.

Male age at the time of mating	Mating duration (min)	Fecundity (No. of eggs)	Percent egg viability	Oviposition period (in days)	Reproductive and non-reproductive period ratio	Reproductive rate (eggs per day)
NE ($n = 10$)	−	−	−	−	−	−
4 ($n = 8$)	52.06 ± 0.46 ab	718.00 ± 2.36 c	83.76 ± 1.83 c	37.38 ± 0.16 b	0.97 ± 0.010 a	20.29 ± 0.080 c
10 ($n = 10$)	102.38 ± 0.32 bc	1 267.60 ± 0.72 e	80.10 ± 0.03 c	53.30 ± 0.04 d	3.73 ± 0.070 a	23.89 ± 0.020 d
20 ($n = 10$)	72.00 ± 1.91 b	1 051.00 ± 1.72 d	76.05 ± 2.78 c	45.70 ± 0.06 c	1.21 ± 0.002 a	23.32 ± 0.040 cd
30 ($n = 10$)	87.50 ± 0.39 b	1 017.50 ± 1.54 d	86.11 ± 0.21 d	40.40 ± 0.07 b	15.69 ± 0.090 b	25.30 ± 0.010 d
40 ($n = 10$)	84.80 ± 0.80 b	1 464.40 ± 2.18 f	82.29 ± 0.21 c	49.60 ± 0.01 c	25.63 ± 0.530 c	29.53 ± 0.040 e
50 ($n = 10$)	96.00 ± 0.38 bc	1 414.50 ± 2.09 f	90.09 ± 0.03 d	47.10 ± 0.02 c	11.10 ± 0.060 b	29.98 ± 0.040 e
60 ($n = 10$)	127.50 ± 2.41 c	555.40 ± 0.42 b	13.15 ± 0.36 a	16.90 ± 0.02 a	3.14 ± 0.005 a	32.93 ± 0.020 f
80 ($n = 10$)	32.60 ± 0.57 a	214.40 ± 0.42 ab	24.40 ± 0.65 b	13.90 ± 0.03 a	7.63 ± 0.020 ab	16.04 ± 0.040 b
100 ($n = 5$)	18.25 ± 0.15 a	64.20 ± 0.51 a	24.77 ± 0.09 ab	11.40 ± 0.04 a	5.93 ± 0.590 ab	5.72 ± 0.060 a
110 ($n = 4$)	28.25 ± 0.53 a	42.80 ± 1.00 a	11.90 ± 0.26 a	10.75 ± 0.31 a	0.77 ± 0.030 a	4.33 ± 0.080 a
F-value	10.68	111.57	54.25	100.86	13.65	52.15

All values are mean ± SE. *F*-values are significant at $P < 0.001$; Data followed by same letters are not statistically significant.

Table 3 Reproductive attributes of *C. sexmaculata* females of varying age when mated singly with 10 day-old males.

Female age at the time of mating	Mating duration (min)	Fecundity (Number of eggs)	Percent egg viability	Oviposition period (in days)	Reproductive and non-reproductive period ratio	Reproductive rate (eggs/day)
NE (*n* = 10)	43.60 ± 0.38 a	1 243.6 ± 3.53 e	74.04 ± 0.38	43.00 ± 0.07 cd	0.74 ± 0.002 a	30.13 ± 0.11 c
10 (*n* = 10)	106.10 ± 0.39 bc	1 267.6 ± 0.72 e	80.10 ± 0.03	53.30 ± 0.04 e	3.73 ± 0.07 ab	23.89 ± 0.02 b
20 (*n* = 10)	70.50 ± 0.65 ab	1 300.8 ± 2.38 e	85.75 ± 0.17	50.80 ± 0.12 de	5.34 ± 0.07 ab	26.31 ± 0.04 bc
30 (*n* = 8)	54.00 ± 1.29 ab	1 354.5 ± 0.87 e	85.35 ± 0.11	55.25 ± 0.05 e	6.18 ± 0.06 ab	24.58 ± 0.03 bc
40 (*n* = 10)	85.00 ± 0.76 ab	1 317.6 ± 0.74 e	87.04 ± 0.05	46.20 ± 0.02 d	4.59 ± 0.01 ab	28.53 ± 0.02 bc
50 (*n* = 4)	74.80 ± 1.25 ab	1 031.0 ± 3.10 d	90.71 ± 0.13	37.75 ± 0.26 c	4.29 ± 0.14 ab	27.50 ± 0.15 bc
60 (*n* = 5)	61.25 ± 0.90 ab	767.2 ± 2.52 c	84.70 ± 0.10	35.00 ± 0.10 c	9.16 ± 0.16 ab	22.06 ± 0.12 ab
80 (*n* = 6)	87.86 ± 1.18 b	275.3 ± 3.87 b	83.65 ± 0.15	19.00 ± 0.23 b	18.59 ± 0.75 b	15.54 ± 0.15 a
100 (*n* = 4)	142.50 ± 1.21 c	202.7 ± 1.53 ab	90.61 ± 0.11	7.50 ± 0.04 a	13.51 ± 0.79 ab	27.00 ± 0.12 bc
110 (*n* = 8)	81.67 ± 1.16 abc	91.6 ± 0.32 a	84.19 ± 0.07	5.25 ± 0.01 a	11.99 ± 0.09 b	17.49 ± 0.05 a
F-value	4.03*	64.63*	0.72	63.72*	2.44**	6.58*

All values are in mean ± SE. *, **, denote significance at $P < 0.001$, $P < 0.05$, respectively. Data followed by same letters are not statistically significant.

and lowest (0.74 ± 0.002) when 10-day-old males mated with 10-day-old females.

Reproductive rate increased up to 60 days, which decreased significantly ($F = 52.15$; df = 14,104; $P < 0.001$) with further increase in male age ($Y = 14.9 + 0.594 X - 0.00657 X^2$; $r = 0.84$; $P < 0.01$; Table 2). However, it decreased ($F = 6.58$; df = 14,104; $P < 0.001$) with increasing female age ($Y = 24.1 + 0.068 X - 0.00107 X^2$; $r = 0.24$; $P < 0.05$; Table 3). A curvilinear increase in reproductive rate was observed with increase in mating duration ($Y = -0.5463 + 0.5217 X - 0.0024 X^2$; $r = 0.59$; $P < 0.005$; Fig. 2). It was highest (32.93 ± 0.02 eggs/day) when 60-day-old males mated with 10-day-old females and lowest (4.33 ± 0.08 eggs/day) when 110-day-old males mated with 10-day-old females.

Female longevity revealed significant positive correlation with reproductive phase delay (Pearson's coefficient (r) = 0.80; $P < 0.01$). This revealed that increased delay in reproductive phase also resulted in increase in female longevity ($Y = 98.9 - 0.207 X + 0.00317 X^2$; $r = 0.84$; $P < 0.001$; Fig. 3).
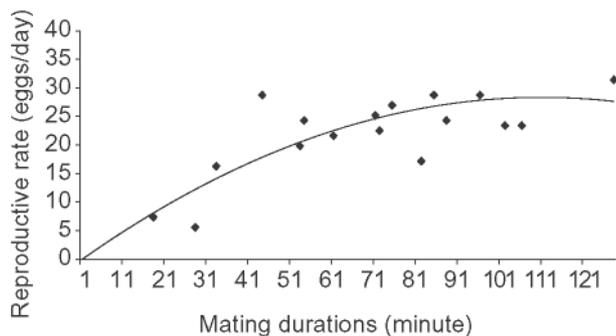

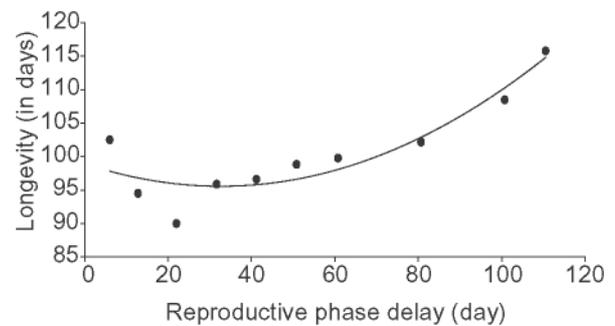**Fig. 3** Relationship between longevity and reproductive phase delay in *C. sexmaculata*.

Fig. 2 Relationship between mating duration and reproductive rate in *C. sexmaculata*.

Discussion

Results reveal increase in percentage mating incidences with increase in both male and female ages. Even NE (8 hours old) females were capable of mating and oviposited after a brief refractory period (*i.e.* 4−6 days). However, early aged males were either incapable of mating (NE to one-day-old) or failed to sire eggs (two-day-old males). High mating incidences with increased reproductive rate in newly emerged females and incapability of early aged (*i.e.* NE to 2 days) males to mate or failure in fertilizing eggs suggest protogyny in *C. sexmaculata*. Protogyny has also

been reported in *Adalia bipunctata* (Linnaeus) (Hemptinne *et al.*, 2001) and *P. dissecta* (Pervez *et al.*, 2004). The strong attraction of older males leading to mating with newly emerged females is similar to that reported earlier in *Leptothea galbula* (Richards, 1980) and *P. dissecta* (Omkar & Pervez, 2002), but disagrees with other reports (Obata, 1988; Majerus, 1994; Hodek & Honek, 1996; Srivastava & Omkar, 2004). Two-day-old males did not fertilize the eggs in females, possibly due to the gonadal immaturity and/or improper intromission of aedeagus.

Increased willingness to mate with increasing male age as evidenced by increasing percent mating incidences could be attributed to their prolonged mate deprivation. Receptivity of females increased with increase in both male and female ages. Six to 10-day-old males were more successful in establishing mating with females. The subsequent successful coercion of females into mating by relatively more mature (*i.e.* 10-day-old) males shows mating in this ladybird to be a male-dominated phenomenon at least in the laboratory. Prolonged ovipositional delay in mated newly emerged females suggests the storage of sperm in spermathecae for laying eggs in future as also found in other ladybird species (Srivastava & Omkar, 2004). Older females oviposited within a few hours after mating, possibly due to presence of mature ova in their ovaries.

Mating duration was male age-dependent as also reported in *C. septempunctata* (Srivastava & Omkar, 2004). Mating in ladybirds was seemingly driven by the male's mating urge as evident by mating with dead females in *Propylea dissecta* (Pervez, 2002) and in this ladybird. Both male and female age at mating affected fecundity as also established previously in *C. septempunctata*, *P. dissecta* and other insects (Srivastava & Omkar, 2004; Mishra & Omkar, 2004; Savalli & Fox, 1998, 1999). Sperm quantity and quality during storage might be acting as constraints on female fecundity that could account for the effect of male age at mating on the female's fecundity. The fecundity increased from NE to 40-day-old females. Lesser fecundity by older females (50 days and above) suggests the onset of senescence (Moore & Moore, 2001), thereby reducing oogenesis due to physiological deterioration. Similarly declining reproductive rate with increasing female age suggests senescence in reproducing females, despite increasing ratio of reproductive and non-reproductive periods with increase in female age. Percent egg viability was unaffected by female age indicating that fertilization of eggs is not affected by female age.

Contrary to the previous study on this ladybird species (Dixon & Agarwala, 2002), percent egg viability did not vary significantly with female age. The prominent effect of male age on percent egg viability might be due to changes in the male's physiology with increasing age, similar to those reported in *C. septempunctata* and *P. dissecta* (Pervez *et al.*, 2004; Srivastava & Omkar, 2004). Reduction in percent egg viability with increasing male age (after 50 days) suggests reduction in sperm supply by aged males, an indication of onset of senescence. Reproductive period and reproductive rate (oviposition capacity) were defined by variations in male age, possibly revealing that ejaculate contents or the quantity of the sperm transferred varies with increasing male age. Male age has a significant role in shaping fecundity, percent egg viability and reproductive rate of females, suggesting that the reproductive performance of females is largely dependent upon the quality of males. The pairing of females with young to intermediate aged males (*i.e.* 10–50 days) may result in maximum reproductive output. Reproductive cessation in males was visible after 50 days PE, whereas in females at the age of 40 days PE. Increased mating duration leads to increased reproductive rate, possibly indicating that eggs laid per day by the females are dependent upon the contribution of males, which in turn is dependent upon duration of mating. This reveals that quantity of sperm transferred during mating is dependent upon mating duration and sperm transfer in this ladybird is probably a continuous process.

Females mating and reproducing till an older age (up to 110 days and more) reflects that though they start senescing early (40 days), their reproductive capacity is not lost completely and they can regain reproduction with more mating stimulus at successive ages.

A linear relationship was found between longevity and reproductive phase delay, suggesting delay in reproductive phase increases life expectancy in this ladybird. Decreased longevity in females reproducing early in life is indicative of the costs of reproduction. Reproductive activity increases stress and oxidative stress susceptibility in *Drosophila* (Salmon *et al.*, 2001; Wang *et al.*, 2001). This provides a possible mechanism for the adverse effects of reproductive activity on somatic fitness and longevity of ladybirds. This trade-off in ladybirds has previously been reported with increased longevity of unmated individuals (Dixon, 2000) and has traditionally been interpreted as a consequence of conflicting demands for resources by reproduction, growth and somatic maintenance. It also evolves as a side effect of the limited combinations of survival and fertility that organisms can achieve at different ages, because of their own biology and the ecological conditions they encounter (Barnes & Partridge, 2003).

Previous studies demonstrate that signals from the brain modulate reproductive maturation and senescence in animals (Golding & Yuwono, 1994; Boulianne, 2001; Braeckman *et al.*, 2001; Finch & Ruvkun, 2001) and an interplay between gonads and brain drives the dynamics of both reproductive phase and senescence (Nelson *et al.*,

1995; Wise *et al.*, 1997), hence, the reproductive cessation (Packer *et al.*, 1998).

Present results reveal that both the sexes mate and reproduce till late ages and thus can be used for mass multiplication. Fifty days for the male and 40 days for the female are the optimum ages up to which the ladybird can reproduce successfully.

It may thus be inferred that: (i) adult age at mating affects various life history attributes in *C. sexmaculata*; (ii) females start mating at the age of 8 hours post-emergence while males after 2 days PE; (iii) male age affects mating duration, fecundity, percent egg viability, ratio of reproductive and nonreproductive periods and reproductive rate; (iv) female age affects fecundity, ratio of reproductive and nonreproductive periods and reproductive rate; (v) reproductive cessation in male ladybirds commences after 50 days PE, whereas in females after 40 days PE; (vi) mating age for optimal reproductive performance is 10−50 days for males and NE to 40 days in females; (vii) higher mating duration elevates reproductive rates; and (viii) commencement of reproduction at an early age reduces the longevity of adults.

Acknowledgments

References

Barnes, A.I. and Partridge, L. (2003) Costing reproduction. *Animal Behaviour*, 66, 199−204.

Beck, C.W. and Powell, L.A., (2000) Evolution of female choice based on male age: Are older males better mates? *Evolutionary Ecology Research*, 2, 107−118.

Boulianne, G.L. (2001) Neuronal regulation of lifespan: clues from flies and worms. *Mechanisms in Aging and Development*, 122, 883−894.

Braeckman, B.P., Houthoofd, K. and Vanfleteren, J.R. (2001) Insulin-like signaling, metabolism, stress resistance and aging in *Caenorhabditis elegans*. *Mechanisms in Aging and Development*, 122, 673−693.

Dixon, A.F.G. and Agarwala, B.K. (2002) Triangular fecundity function and ageing in ladybird beetles. *Ecological Entomology*, 27, 433−440.

Dixon, A.F.G. (2000) *Insect Predator-Prey Dynamics: Ladybird beetles and Biological Control.* Cambridge University Press, Cambridge. p. 257.

Finch, C.E. and Ruvkun, G. (2001) The genetics of aging. *Annual Reviews of Genomics and Human Genetics*, 2, 435−462.

Golding, D.W. and Yuwono, E. (1994) Latent capacities for gametogenic cycling in the semelparous invertebrate. *Proceedings of National Academy of Science USA*, 91, 11777−11781.

Hansen, T.F. and Price, D.K. (1995) Good genes and old genes. Do old mates provide superior genes? *Journal of Evolutionary Biology*, 8, 759−778.

Heinninger, K. (2002) Aging is a deprivation syndrome driven by a germ-soma conflict. *Ageing Research Reviews*, 1, 481−536.

Hemptinne, J.-L., Dixon, A.F.G. and Adam, B. (2001) Do males and females of the two-spot ladybird, *Adalia bipunctata* (L.), differ in when they mature sexually. *Journal of Animal Behaviour*, 14, 411−419.

Hodek, I. and Honek, A. (1996) *Ecology of Coccinellidae*. Dordrecht: Kluwer Academic Publishers. p. 464.

Johnson, T.E., Mitchell, D.H., Kline, S., Kemal, R. and Foy, J. (1984) Arresting development arrests aging in the namatode *Caenorhabditis elegans*. *Mechanisms in Ageing and Development*, 28, 23−40.

Jones, T.M., Balmford, A. and Quinnell, R.J. (2000) Adaptive female choice for middle-aged mates in a lekking sandfly. *Proceedings of Royal Society London, Series B*, 267, 681−686.

Kokko, H., and Lindstrom, J. (1996) Evolution of female preference for old mates. *Proceedings of Royal Society London, Series B*, 263, 1533−1538.

Majerus, M.E.N. (1994) Female promiscuity maintains high fertility in ladybirds (Coleoptera: Coccinellidae). *Entomologist's Monthly Magazine*, 130, 205−209.

Mangel, M. (2002) Complex adaptive system, aging and longevity. *Journal of Theoretical Biology*, 213, 559−571.

Manning, J.T. (1985) Choosy females and correlates of male age. *Journal of Theoretical Biology*, 116, 349−354.

Minitab (2003) *Minitab Statistical Software*, Minitab Release 13.2, Minitab Inc.

Mishra, G. and Omkar (2004) Influence of parental age on reproductive performance of an aphidophagous ladybird, *Propylea dissecta* (Mulsant). *Journal of Applied Entomology*, 28 (9−10), 605−609.

Mishra, G. and Omkar (2006) Ageing trajectory and longevity trade-off in a generalist aphidophagous ladybird, *Propylea dissecta* (Coleoptera: Coccinellidae). *European Journal of Entomology*, 103, 33−40.

Moore, P.J. and Moore, A.J. (2001) Reproductive ageing and mating: the ticking of the biological clock in female cockroaches. *Proceedings of National Academy of Science USA*, 98, 9171−9176.

Nelson, J.F., Karelus, K., Burgman, M.D. and Felicio, L.S.

(1995) Neuroendocrine involvement in aging: evidence from studies of reproductive aging and caloric restriction. *Neurobiology of Aging*, 16, 837−843.

Obata, S. (1988) Mating refusal and its significance in female of the ladybird beetle, *Harmonia axyridis. Journal of Physiological Entomology*, 13, 193−199.

Omkar and Bind, R.B. (2004) Prey quality dependent growth, development and reproduction of a biocontrol agent, *Cheilomenes sexmaculata* (Fabricius) (Coleoptera: Coccinellidae). *Biocontrol Science and Technology*, 14, 665−673.

Omkar and Bind, R.B. (1993) Records of aphid-natural enemies complex of Uttar Pradesh. II. The Coccinellids. *Journal of Advance Zoology*, 14(2), 96−99.

Omkar and Mishra, G. (2005) Mating in aphidophagous ladybirds: costs and benefits. *Journal of Applied Entomology*, 129, 432−436.

Omkar and Pervez, A. (2002) Influence of temperature on the age-specific fecundity of a ladybird beetle, *Micraspis discolor* (Fabricius). *Insect Science and its Application*, 22, 61−65.

Omkar and Pervez, A. (2005) Mating behavior of an aphidophagous ladybird beetle, *Propylea dissecta* (Mulsant). *Insect Science*, 12, 37−44.

Omkar, Singh, S.K., Pervez, A. and Mishra, G. (2004) Age-specific fecundity and natality life-table of an aphidophagous ladybird, *Cheilomenes sexmaculata. Biological Memoirs*, 30, 20−25.

Packer, C., Tartar, M. and Collins, A. (1998) Reproductive cessation in female mammals. *Nature*, 392, 807−811.

Pervez, A. (2002) Contribution on prey-predator relationship and reproductive biology of a colour morph of *Propylea dissecta* (Mulsant) (Coccinellidae: Coleoptera). PhD Thesis, University of Lucknow, Lucknow, India.

Pervez, A., Omkar and Richmond, A.S. (2004) The influence of age on reproductive performance of the predatory ladybird beetle, *Propylea dissecta*. 8pp. *Journal of Insect Science*, 4: 22.

Richards, A.M. (1980) Sexual selection, guarding and sexual conflict in a species of Coccinellidae (Coleoptera). *Journal of Australian Entomological Society*, 19, 26.

Rose, A.R. (1984) Laboratory evolution of postponed senescence in *Drosophila melanogaster. Evolution*, 38, 1004−1010.

Salmon, A.B., Marx, D.B. and Harshman, L.G. (2001) A cost of reproduction in *Drosophila melanogaster*: stress susceptibility. *Evolution*, 55, 1600−1608.

Savalli, U.M. and Fox, C.W. (1998) Genetic variation in paternal investment in a seed beetle. *Animal Behaviour*, 56, 953−961.

Savalli, U.M. and Fox, C.W. (1999) The effect of male size, age and mating behaviour on sexual selection in the seed beetle *Collasobruchus maculates. Ethology Ecology and Evolution*, 10, 49−60.

Sgro, C.M. and Partridge, L. (1999) A delayed wave of death from reproduction in *Drosophila. Science*, 286, 2521−2524.

Srivastava, S. and Omkar (2004) Age specific mating and reproductive senescence in seven spotted ladybird, *Coccinella septempunctata. Journal of Applied Entomology*, 128, 452−458.

Tao, C.C. and Chiu, S.C. (1971) Biological control of citrus, vegetables and tobacco aphids. *Special Publication of Taiwan Agricultural Research Institute*, 10, 1−110.

Tartar, M. and Yin, C.M. (2001) Slow aging during insect reproductive diapause: why butterflies, grasshoppers and flies are like worms. *Experimental Gerontology*, 36, 723−738.

Wang, Y., Salmon, A.B. and Harshman, L.G. (2001) A cost of reproduction: oxidative stress susceptibility is associated with increased egg production in *Drosophila melanogaster. Experimental Gerontology*, 36, 1349−1359.

Wise, P.M., Kashon, M.L., Krajnak, K.M., Rosewell, K.L., Cai, A., Scarbrough, K., Harney, J.P., McShane, T., Lloyd, J.M. and Weiland, N.G. (1997) Aging of the female reproductive system: a window into brain aging. *Recent Progress in Hormonal Research*, 52, 279−303.