

Age-specific mating and reproductive senescence in the seven-spotted ladybird, *Coccinella septempunctata*

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Abstract: Adults of the seven-spotted ladybird, *Coccinella septempunctata* Linnaeus (Col., Coccinellidae) were paired for mating from very young to old age (1–50 days) to record the willingness to mate, attainment of sexual maturity and onset of reproductive senescence in both the sexes. Mating commenced after 4 and 2 days of emergence of male and female, respectively, and 100% mating was achieved at the young age in both cases (10 days). Willingness to mate decreased with increase in the age from 40 to 50 days of both the sexes. Ladybird exhibited protandry. Mating duration, fecundity and per cent viability of eggs of middle-aged males (20–30 days old) and females (20 days old) were the highest. Mating duration and per cent viability of eggs were male age dependent, whereas pre-oviposition and oviposition periods were mating stimulus dependent. Oviposition period and fecundity were female age-dependent responses. Fecundity was highest when 20-day-old female and 30-day-old male were paired. Onset of reproductive senescence started at the age of 30 days in males and 20 days in females. The present study confirms the effect of ageing on male and female *C. septempunctata* and supports the Hansen and Price [J. Evol. Biol. (1995) vol. 8, pp. 759–778] model that females mating with young and middle-aged males yield optimal quality progeny.

Key words: *Coccinella septempunctata*, ageing, ladybird, mating incidence, reproduction, reproductive senescence

1 Introduction

Ageing has been reconized as a declining change from maturity to senescence (ROTHSTEIN, 1982) and is widely studied in insects. The decline in the force of natural selection with increasing age may also be one of the reasons for ageing (MEDAWAR, 1946), whereas, evolutionary theory depicts that ageing is a response to the pattern of externally imposed hazards on survival and fertility (PRIEST et al., 2002).

Three theories predict the influence of age on mate choice and fecundity in insects with respect to male age. The viability indicator model or good genes model predicts that females prefer older males (of higher genotypic quality) to younger males (TRIVERS, 1972; MANNING, 1985; KIRKPATRICK, 1987; ANDERSON, 1994; KOKKO and LINDSTROM, 1996). The HANSEN and PRICE (1995) model proposes reduction in progeny output on pairing with older males, with a simulation model predicting that middle-aged males will be preferred to others (BECK and POWELL, 2000; JONES et al., 2000). A few age-related studies have also focussed on the effects of maternal and paternal age on ageing of offsprings (PRIEST et al., 2002; TREGENZA et al., 2003), whereas others have explained ageing in terms of a trade-off between fecundity and longevity of insects (SGRO and

PARTRIDGE, 1999; ROBINE and VAUPEL, 2001; BARNES and PARTRIDGE, 2003).

Most studies on ladybirds focus on prey–predator interactions, predator's searching efficiency and general life history (HODEK and HONEK, 1996; HODEK and CERYNGIER, 2000), whereas only a few studies have addressed reproductive behaviour and reproduction (OBATA, 1987; ISOGAI et al., 1990; OBATA and JOHKI, 1991; DIXON and KUNDU, 1997; DIXON and AGARWALA, 2002; OMKAR and PERVEZ, 2002; OMKAR and SRIVASTAVA, 2002). The need for an intensive study on sexual activity and reproduction in ladybirds has recently been expressed (HODEK and CERYNGIER, 2000).

Although a number of studies on age and ageing in insects have been conducted (MANGEL, 2001; HEININGER, 2002; KIRKWOOD, 2002; PRIEST et al., 2002), it is still a less-studied aspect in ladybirds with only a few age-related studies on age-specific fecundity, walking speed, predation and clutch size (PONSONBY and COPLAND, 1998; DIXON and AGARWALA, 2002; OMKAR and PERVEZ, 2002). This prompted us to study age as an indicator of quality of individual and its effect on attainment of sexual activity, optimal reproduction and onset of reproductive senescence in the seven-spotted ladybird, *Coccinella septempunctata*

Linnaeus, one of the most common ladybirds worldwide and a predominant generalist predator of aphids.

2 Materials and Methods

2.1 Stock maintenance

Individuals of *C. septempunctata* along with aphid, *Aphis craccivora* Koch from host plant, *Dolichos lablab* Linnaeus were collected from local agricultural fields and reared in the laboratory [$25 \pm 2^\circ\text{C}$, $60 \pm 5\%$ relative humidity (RH) and 12.00 : 12.00 hours (light : day)]. Adults were paired in Petri dishes on *ad libitum* *A. craccivora* and allowed to mate. The eggs laid were collected and reared from hatching to adult emergence in glass beakers (11.0 × 9.0 cm) on daily replenishment of *A. craccivora*-infested on *D. lablab* twig. The emerging adults were sexed and used in experiments. All experiments were performed under abiotic conditions similar to that of stock culture.

2.2 Age-specific willingness to mate

Newly emerged adults of *C. septempunctata* were sexed and kept separately in Petri dishes (9 cm × 1.5 cm) to maintain their unmated status for 1, 2, 4, 6, 8, 10, 20, 30, 40 and 50 days. To record the onset of sexual activity in males, 1-day-old unmated male was paired with 1-day-old virgin female in a Petri dish at 10.00 hours. The responses of male and female were observed continuously for 30 min and then after every hour till 18.00 hours. If mating occurred, its duration was carefully recorded. Only single mating was allowed and individuals were separated post-mating and the female isolated for observation for post-mating response in terms of eggs laid and their viability. This procedure was repeated 10 times to record mating incidences in each set. One-day-old males were similarly paired with 2-, 4-, 6-, 8-, 10-, 20-, 30-, 40- and 50-day-old virgin females. The experiment was also repeated with unmated 2-, 4-, 6-, 8-, 10-, 20-, 30-, 40- and 50-day-old males. Mating incidences at different ages of adults were analysed by the chi-square test, correlated with age of both sexes and the age-specific willingness to mate was determined.

The willingness to mate was determined using following formula:

$$W = \frac{N1 \times 100}{N}$$

where, W is the willingness (%) of a partner (male and female) to mate, $N1$ the number of individuals of same age that mated with counterparts of varying ages, and N the number of individuals of same age that were paired with the counterparts of varying ages (here, $n = 100$, as there were 10 set-ups of varying ages in 10 replicates).

2.3 Sexual maturity and reproductive senescence

To predict sexual maturity and reproductive senescence in both sexes, isolated females (isolated after single mating from above experiment) were further observed. They were reared for their lifetime on daily replenished *A. craccivora*. The adults were predicted to reach sexual maturity at the age when 50% mating was achieved; the initial age at which mating first occurred (2 days) and age at which 100% mating was achieved (10 days) acting as the two extremes between which observations were taken. Pre-oviposition, oviposition

and post-oviposition periods, fecundity and per cent viability of eggs of each set were recorded to determine the age of start of reproductive senescence.

As a result of mating in only small fractions in younger adults (1–8 days), they were excluded from statistical analysis. Data of 10-day-old males with females of different ages, viz. 10, 20, 30, 40 and 50 days old and vice versa were subjected to one-way ANOVA followed by Tukey's *post hoc* test of significance and linear regression.

To analyse the overall effect of age of male and female, data were pooled into three groups: young, middle and old ages. In case of male, young (1–10 days), middle age (20–30 days), and old (40–50 days) and in females, young (1–10 days), middle age (20 days) and old (30 days) groups were formed and one-way ANOVA and linear regression were applied. As a result of the non-responsiveness of 40- and 50-day-old females, in terms of reproductive output, with males of different ages they were omitted from statistical analysis, but mating duration of these females with males of different ages were analysed. Analyses were performed using the statistical software MINITAB (Minitab Inc., Philadelphia, USA) on personal computer.

3 Results

3.1 Age-specific willingness to mate

Newly emerged males (1–2 days old) did not mate. Mating started in 4-day-old males and increased upto 100% at the age of 10 days. In females, mating started relatively earlier (2 days) than in males (4 days); 20% mating occurred between 2-day-old females and 8-day-old males. Mating incidences of 10-day-old females were more (90, 100, 70 and 10%) than the males (100, 70, 50, and 0%) with 20, 30, 40 and 50-day-old males and females, respectively (table 1).

The willingness to mate was observed after 4 and 2 days of emergence in males and females, respectively. Ten-day-old males and females were most willing to mate; 8-, 10- and 20-day-old females were more willing to mate than the same aged males and 30-, 40- and 50-day-old males were more willing to mate than the same aged females. Willingness to mate in males and females started decreasing after the age of 30 and 20 days, respectively (fig. 1).

3.2 Sexual maturity and reproductive senescence

Graphical interpretation revealed that the males matured sexually at the age of 8.9 days and females at the age of 9.8 days, revealing slight protandry in the ladybird (fig. 2). Mating duration of young females was significantly different with males of varying ages ($F = 13.60$; d.f. = 4, 25; $P < 0.001$; table 2). Mating duration of middle-aged female with middle-aged males was the highest (70.00 ± 4.50 min) ($F = 6.10$; d.f. = 3, 20; $P < 0.001$; table 2). Differences in mating durations of old female with young and middle-aged males were also significant and the mating duration was the lowest with old males (38.33 ± 2.93 min) ($F = 3.14$; d.f. = 3, 20; $P < 0.05$; table 2; fig. 3).

The pre-oviposition periods of young, middle-aged and old females did not vary significantly with increase

Table 1. The number of males and females of *C. septempunctata* of increasing age that copulated with 1-, 2-, 4-, 6-, 8-, 10-, 20-, 30-, 40- and 50-day-old females and males ($n = 10$)

Male age (days)	Female age (days)										χ^2 (P-value)	
	1	2	4	6	8	10	20	30	40	50		
1	0	0	0	0	0	0	0	0	0	0	0	–
2	0	0	0	0	0	0	0	0	0	0	0	–
4	0	0	2	2	4	4	0	0	0	0	0	14.541 (0.106)
6	0	0	2	3	5	5	4	4	3	0	0	12.041 (0.213)
8	0	2	4	5	5	7	1	1	0	0	0	9.786 (0.369)
10	0	2	4	5	7	10	10	7	5	0	0	16.361 (0.061)
20	0	0	0	4	4	9	10	7	4	1	1	24.814 (0.003)
30	0	0	0	4	6	10	7	7	4	1	1	19.599 (0.021)
40	0	0	2	3	6	7	4	4	3	0	0	17.161 (0.047)
50	0	0	0	0	1	1	3	2	0	0	0	7.418
χ^2 (P-value)	–	–	19.454 (0.022)	14.123 (0.120)	16.388 (0.061)	19.655 (0.355)	23.396 (0.006)	18.733 (0.029)	18.733 (0.029)	12.259		

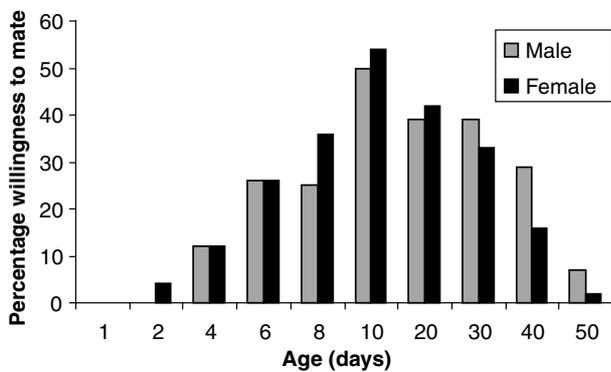


Fig. 1. Willingness to mate of male and female *C. septempunctata* of varying age

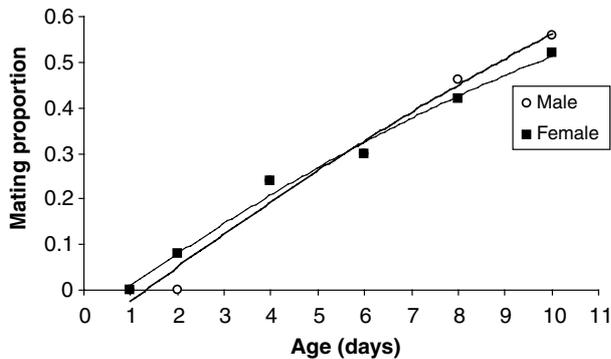


Fig. 2. Predicted age of sexual maturity in male and female *C. septempunctata*

in male age ($F = 1.69$; d.f. = 4, 25; $P < 0.1$; $F = 2.25$; d.f. = 3, 20; $P < 0.1$; $F = 3.21$, d.f. = 3, 20; $P < 0.05$; table 2). The oviposition periods of young and middle-aged females were more significantly different ($F = 36.93$; d.f. = 4, 25; $P < 0.001$; $F = 5.63$; d.f. = 3, 20; $P < 0.001$) than the old females with different age groups of males ($F = 1.82$; d.f. = 3, 20; $P < 0.01$; table 2; fig. 4).

Fecundities of young, middle-aged and old females were significantly different when mated with males of

different age groups ($F = 66.85$; d.f. = 4, 25; $P < 0.001$; $F = 13.57$; d.f. = 3, 20; $P < 0.001$; $F = 4.83$; d.f. = 3, 20; $P < 0.01$; table 2; fig. 5). Per cent viability of eggs increased with increase in male age upto 30 days, thereafter declined in older males. Per cent egg viability of different aged females with young, middle-aged and old males was significantly different ($F = 9.94$; d.f. = 4, 25; $P < 0.001$; $F = 63.60$; d.f. = 3, 20; $P < 0.001$; $F = 7.17$; d.f. = 3, 20; $P < 0.001$; table 2; fig. 6). Post-oviposition periods of young and old females with the three age groups of males were significantly different ($F = 7.23$; d.f. = 4, 25; $P < 0.001$; $F = 1.43$; d.f. = 3, 20; $P < 0.05$), although in the middle-aged females, the differences in post-oviposition periods were not significant ($F = 0.86$; d.f. = 3, 20; $P < 0.05$; table 2).

Table 3 reveals relationships between the different age groups of female with males of different ages. Mating duration and oviposition period of young females vary significantly than the middle-aged and old females ($P < 0.001$). Fecundity of all three groups of females varied significantly with the three age groups of males ($P < 0.001$). Per cent egg viability, however, was not female age dependent as it did not differ significantly ($P < 1$; table 3).

ANOVA revealed overall highly significant effect of male age on mating duration and per cent viability of eggs fertilized by young and old males ($F = 31.97$; d.f. = 2, 105; $P < 0.001$; $F = 40.02$; d.f. = 2, 51; $P < 0.001$). Regression equations of mating duration and per cent viability of eggs with different age groups of male were $Y = 61.4 - 4.69X$; $R^2 = 0.0710$; $P = 0.005$ and $Y = 97.9 - 4.55X$; $R^2 = 0.2940$; $P < 0.001$, respectively.

Pre-oviposition, oviposition, and post-oviposition periods varied significantly with the age of females ($F = 713.72$; d.f. = 2, 69; $P < 0.001$; $F = 37.29$; d.f. = 2,69; $P < 0.001$; $F = 22.79$; d.f. = 2,69; $P < 0.001$) and their relationship with the females' age was $Y = 1.94 + 10.9X$, $R^2 = 0.9540$; $P < 0.001$; $Y = 29.6 - 5.89X$; $R^2 = 0.4900$; $P < 0.001$; $Y = 16.8 - 2.40X$; $R^2 = 0.2730$; $P < 0.001$, respectively. Fecundity also varied significantly with the age of females ($F = 36.13$; d.f. = 2, 69; $P < 0.001$;

Table 2. Biological attributes of different aged females of *C. septempunctata* with males of different pooled age

Female age (in days)	Male age when mated	Mating duration (in min)	Pre-oviposition period (in days)	Oviposition period (in days)	Fecundity (in eggs)	Per cent viability	Post-oviposition period (in days)
10	10	52.50 ± 1.13	12.17 ± 0.00	29.50 ± 1.13	312.83 ± 0.45	91.66 ± 0.92	14.00 ± 1.35
	20	66.00 ± 1.80	12.67 ± 0.00	27.40 ± 0.45	256.16 ± 16.65	92.67 ± 0.84	15.17 ± 2.70
	30	68.67 ± 1.80	12.33 ± 0.68	25.17 ± 0.90	253.16 ± 5.86	94.33 ± 0.24	13.00 ± 0.45
	40	56.33 ± 2.70	13.33 ± 0.23	17.50 ± 0.23	150.38 ± 5.85	86.76 ± 2.61	20.33 ± 0.45
	50	31.33 ± 1.35	13.83 ± 0.90	10.50 ± 1.58	78.83 ± 17.10	78.11 ± 5.92	19.50 ± 1.35
	F-value	13.60*	1.69****	36.93*	66.85 *	9.94*	7.23*
20	10	48.00 ± 5.85	23.33 ± 0.23	22.33 ± 1.13	291.17 ± 13.95	90.92 ± 0.55	9.00 ± 0.45
	20	65.00 ± 5.85	23.50 ± 0.45	22.50 ± 0.68	290.67 ± 15.75	92.42 ± 0.63	9.00 ± 0.45
	30	70.00 ± 4.50	22.66 ± 0.45	18.00 ± 0.45	281.33 ± 16.20	94.13 ± 0.38	11.00 ± 0.45
	40	40.33 ± 0.45	25.50 ± 0.45	15.33 ± 0.00	202.83 ± 0.45	79.04 ± 0.43	9.00 ± 0.45
	F-value	6.10*	2.25****	5.63*	13.57*	63.60*	0.86****
30	10	53.00 ± 5.85	33.00 ± 0.45	12.67 ± 0.68	167.50 ± 3.38	89.29 ± 0.17	12.00 ± 0.00
	20	58.67 ± 5.18	34.83 ± 0.23	12.57 ± 0.68	165.00 ± 5.40	93.07 ± 1.34	12.50 ± 1.13
	30	65.00 ± 1.35	36.67 ± 0.00	9.83 ± 0.90	127.67 ± 4.28	94.11 ± 0.08	14.50 ± 0.23
	40	38.33 ± 2.93	34.00 ± 0.23	9.50 ± 1.13	113.00 ± 16.20	80.10 ± 2.35	11.00 ± 1.80
	F-value	3.14***	3.21***	1.82**	4.83**	7.17*	1.43****

Values are mean ± SE.
Values significant at *P < 0.001; **P < 0.01; ***P < 0.05; ****P < 0.1.

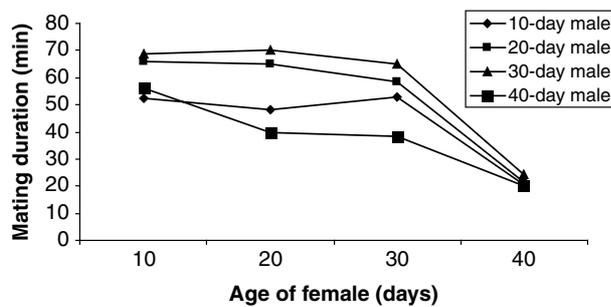
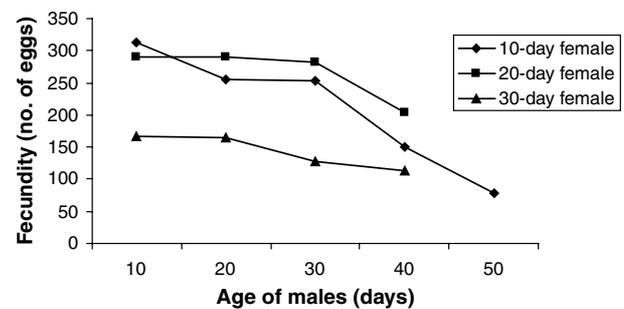
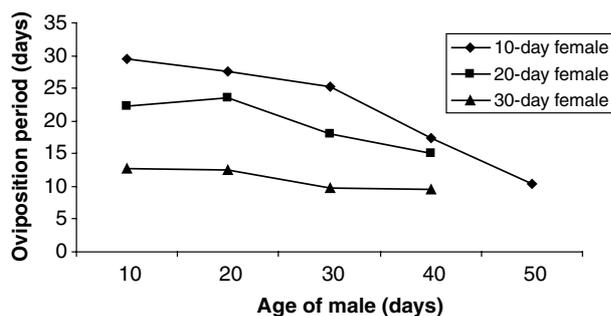
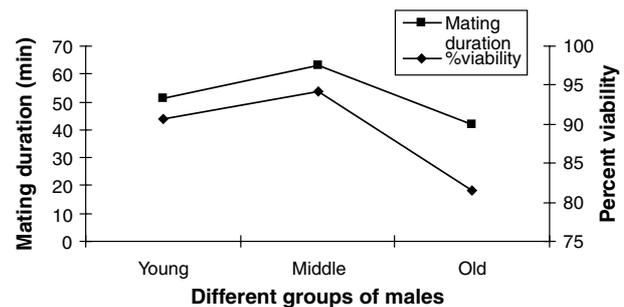
**Fig. 3.** Mating duration of males of different ages with the females of different ages**Fig. 5.** Fecundity of females of different ages when mated with the males of different ages**Fig. 4.** Oviposition period of females when mated with males of different ages**Fig. 6.** Mating duration and per cent viability of different age groups of males in *C. septempunctata*

fig. 7) and the relationship between fecundity and female age can be depicted by the regression equation $Y = 307 - 46.0X$; $R^2 = 0.2640$; $P < 0.001$.

4 Discussion

Younger (1–2-day-old) males and females were unwilling to mate. Lack of elytral hardening and incomplete

pigmentation in females up may be responsible for the unresponsiveness of males towards newly emerged to 2-day-old females. This has also been reported earlier (OBATA, 1988; MAJERUS, 1994; HODEK and HONEK, 1996; OMKAR and SRIVASTAVA, 2002). However, in the ladybird, *Leptothea galbula* (Mulsant) males were strongly attracted towards female pupae and mounted immediately after female emergence, but mating occurred (1 h after eclosion) only after hardening of female elytra (RICHARDS, 1980).

Factor	Stage of female	Regression equation	R ² -value	P-value
Mating duration	Young	$Y = 123 - 8.17X$	0.4860	0.001
	Middle-aged	$Y = 104 - 3.85X$	0.0870	0.1
	Old	$Y = 103 - 3.23X$	0.0690	0.2
Oviposition Period	Young	$Y = 60.40 - 4.80X$	0.7910	0.001
	Middle-aged	$Y = 44.80 - 2.02X$	0.2540	0.01
	Old	$Y = 31.50 - 1.23X$	0.1800	0.05
Fecundity	Young	$Y = 671 - 57.6X$	0.8580	0.001
	Middle-aged	$Y = 609 - 27.4X$	0.4620	0.001
	Old	$Y = 475 - 20.1X$	0.3810	0.001
Per cent viability	Young	$Y = 91.30 - 0.012X$	0.0010	1
	Middle-aged	$Y = 90.7 + 0.20X$	0.0060	1
	Old	$Y = 95.6 - 0.11X$	0.0020	1

Table 3. Regression equations of constant age female of *C. septempunctata* with 10-, 20-, 30-, 40- and 50-day-old males on mating duration, oviposition period, fecundity and per cent viability

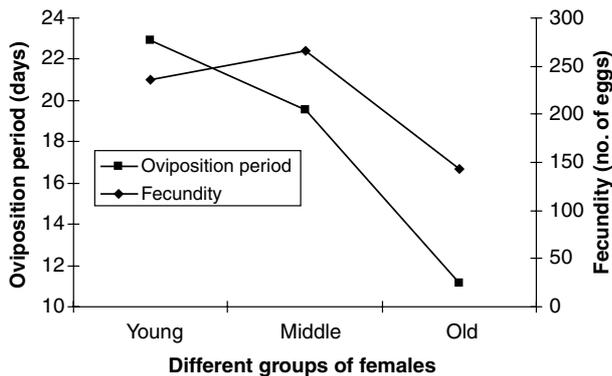


Fig. 7. Oviposition period and fecundity of different age groups of females in *C. septempunctata*

Increased willingness to mate in both the sexes of ladybirds was noticed after 4 days post-emergence. Neurosecretory materials accumulate and activate the receptivity centre in the brain for a few days after emergence leading to stimulation for mating in cockroaches and during this time corpus allatum is inhibited by neuro-signals from the brain, leading to low oocyte maturation and yolk deposition. The coordinated activity of the receptivity centre and corpus allatum facilitates mating even when oocytes are small and some yolk is deposited (MOORE and MOORE, 2001). The same may be true for ladybirds and could be the reason for the delayed willingness to mate in *C. septempunctata*. The post-emergence refractory period of males and females also reduces the risk of mating with siblings (ANTOLIN and STRAND, 1992) and the incidence of inbreeding depression (MORJAN et al., 1999).

Males of 4 days of age or more were more responsive towards 8-, 10-, 20-, 30-day-old females. Response of male to these females was probably the result of change in visual and chemical cues of mature females. Mature females (8-, 10-, 20- and 30-day-old) mated more frequently than the young females (as evident by the increased willingness quotient). It may be possible that mature females reduced the mating rejections, which may be a response to the increasing age as delay in mating may probably lead to a permanent decline in the reproductive quality of females (MOORE and MOORE, 2001).

Middle-aged males had the highest mating incidence, which may be a result of prolonged mate deprivation. Decline in the willingness to mate and mating duration with the advancement of age perhaps indicates the onset of senescence in males. Reproductive status of the female also affects the stimulation of male, as in *Pyrhocoris apterous* (Heteroptera), in which the reproductive activity of the male is enhanced by more than 10 days in the presence of reproductively active females than in the presence of reproductively senescent females (HODKOVA et al., 1991). Physiological state, age and age difference between the two sexes of the ladybirds were responsible for differences in the sexual activity of ladybirds (OMKAR and SRIVASTAVA, 2002; A. PERVEZ and OMKAR, unpublished observations; A. OMKAR and G. MISHRA, unpublished observations).

Lack of oviposition in 2- to 6-day-old females of *C. septempunctata* after mating may be attributed to the time needed for the development of eggs. The results corroborated the existence of protandry in *C. septempunctata* (OMKAR and SRIVASTAVA, 2002), *Harmonia axyridis* (OBATA, 1987), *Cheilomenes sexmaculata* (BIND, 1998) and *Propylea dissecta* (PERVEZ and OMKAR, unpublished observations). It has been suggested that if species have overlapping generations and females mate several times during their lifetime then there can be no advantage in males emerging and maturing sexually earlier than females (DIXON, 2000). A slight protogyny has however been reported in *Adalia bipunctata* (HEMPINNE et al., 2001).

Mature females oviposited just after a few hours of mating; this indicates the presence of mature ova in their reproductive tract. Old females show the decline in fecundity. Thus, oviposition pattern of ladybirds shows three stages, maturation, maturity and senescence. At maturity, egg laying starts, reaches its peak and then declines.

The single-mated females were found to be less fecund than those which mated several times. Single mating does not maximize female fitness and the positive effects of remating on egg production rate may be attributed to the stimulating or gonadotropic effects of mating (ARNQVIST and NILSSON, 2000). Longer post-oviposition period of younger females than of the older ones suggests that cessation of oviposition was temporary and re-mating can again induce oviposition in ladybirds. Multiple matings increase the fecundity of *C. septempunctata* (OMKAR and SRIVASTAVA, 2002). The

fecundity of single-mated females of *C. septempunctata* was found to be comparatively lower than the single-mated *P. dissecta* (PERVEZ, 2002).

The highest fecundity was recorded at the age of 20 days and per cent viability was maximum after mating with males aged 30 days. These results again reveal asynchrony in the maturation of male and female ladybirds. Asynchrony in the initiation of gonadal maturation was also reported earlier (ISOGAI et al., 1990; CERYNGIER et al., 1992; OMKAR and SRIVASTAVA, 2002) but at the middle age this asynchrony in the level of gonadal maturation disappears (DIXON, 2000). This asynchrony may be ascribed to the difference in food consumption, assimilation and rate of metabolism. The effect of asynchrony on reproduction has been studied in detail in *P. dissecta* (OMKAR and MISHRA, unpublished observations).

Selection against old females is also related to mate choice, as choice of old females by males may lead to loss of sperm because of their reduced fecundity. Similarly no mating between older females and old males may be a result of senescence. Influence of male age on fecundity of female *C. septempunctata* supports the study on other insects, viz., seed beetle *Stator limbatus* and *Callosobruchus maculatus* in which varying male age has a seemingly significant role in shaping the fecundity of females (SAVALLI and FOX, 1998, 1999). During the insemination process of *C. septempunctata*, the sperms are transferred via a sac-like spermatophore, which is usually ejected by the female after copulation (OBATA and JOHKEI, 1991; OMKAR and SRIVASTAVA, 2002). Thus, essential nutrients may be transferred via a spermatophore resulting in increased female fitness. The females inseminated by old males might probably receive a small ejaculate and fewer nutrients. An effect of male age on ejaculate size has previously been found in *C. maculatus* (FOX et al., 1995). The present finding supports the view that there is genetic variation in male investment (SAVALLI et al., 2000) and that females use nutrients within the ejaculates during oogenesis (THORNHILL and ALCOCK, 1983; FOX et al., 1995; SAVALLI and FOX, 1998, 1999).

The decline in viability of eggs fertilized by old males also suggests a possible decrease in sperm count in old males showing a senescence trajectory, which may be responsible for selection for young and middle-aged males and females against old ones. These findings agree with the HANSEN and PRICE (1995) model that young and middle-aged males are better quality mates. Although a few studies suggest that male genetic quality remains constant with age (BECK and POWELL, 2000), our findings suggest male genetic quality decreases after a certain age. It could be due to rates of deleterious mutation higher in older males than in young ones (HANSEN and PRICE, 1995; CROW, 1997). The decline in mating and post-mating responses of both the sexes of ladybird with age reveals that along with many other constraints of life history, senescence also regulates physiology (e.g. rate of metabolism) of the organism and these changes from the maturity through senescence constitute the ageing process (ROTHSTEIN, 1982). Early senescence in females may be attributed to the constraint of fecundity.

Conclusions

(i) Males were willing to mate at the age of 4 days and females at the age of 2 days. (ii) 100% adults were willing to mate at the age of 10, 20 and 30 days. (iii) *C. septempunctata* shows slight protandry, males mature slightly earlier than the females. (iv) 2–6-day-old females although mated did not oviposit. (v) Young males preferred young females. (vi) Middle-aged males mated more successfully with the young females. (vii) Mating duration and per cent viability of eggs were male age dependent and declined after the male age of 30 days. (viii) Fecundity was female age dependent, and it was maximum at the female age of 20 days. (ix) Maximum fecundity can be achieved by pairing the 20-day-old female with 30-day-old male. (x) Senescence in male and female ladybird started after 30 and 20 days of emergence, respectively.

The results of this study can be exploited in mass multiplication practices for propagation of *C. septempunctata* by identifying optimum age for reproduction thereby allowing formation of optimum aged pairs for maximum progeny output. Similar studies on other biological control agents would also help pave the way for effective mass multiplication.

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References

- ANDERSON, M., 1994: Sexual Selection. Princeton, NJ: Princeton University Press.
- ANTOLIN, M. F.; STRAND, M. R., 1992: Mating system of *Bracon hebetor* (Hymenoptera: Braconidae). Ecol. Entomol. **17**, 1–7.
- ARNQVIST, G.; NILSSON, T., 2000: The evolution of polyandry: multiple mating and female fitness in insects. Anim. Behav. **60**, 145–164.
- BARNES, A. I.; PARTRIDGE, L., 2003: Costing reproduction. Anim. Behav. **64**, 199–204.
- BECK, C. W.; POWELL, L. A., 2000: Evolution of female choice based on male age: are older males better mates? Evol. Ecol. Res. **2**, 107–118.
- BIND, R. B., 1998: Bioecology and behaviour of a ladybird beetle, *Cheilomenes (=Menochilus) sexmaculata* (Fabricius) (Coleoptera: Coccinellidae). Ph.D. Thesis. Lucknow: University of Lucknow, pp. 164.
- CERYNGIER, P.; KINDLMANN, P.; HAVELKA, J.; DOSTALKOVA, I.; BRUNHOFER, V.; HODEK, I., 1992: Effect of food, parasitization, photoperiod and temperature on gonads and sexual activities of males of *Coccinella septempunctata* (Coleoptera: Coccinellidae) in autumn. Acta Entomologica Bohemoslovaca **89**, 97–106.
- CROW, J. F., 1997: The high spontaneous mutation rate: is it a health risk? Proc. Natl Acad. Sci. USA **94**, 8380–8386.
- DIXON, A. F. G., 2000: Insect Predator–Prey Dynamics: Ladybird Beetles and Biological Control. Cambridge: Cambridge University Press.

- DIXON, A. F. G.; AGARWALA, B. K., 2002: Triangular fecundity function and ageing in ladybird beetles. *Ecol. Entomol.* **27**, 433–440.
- DIXON, A. F. G.; KUNDU, R., 1997: Trade-off between reproduction and length of adult life in males and mating females of aphids. *Eur. J. Entomol.* **94**, 105–109
- FOX, C. W.; HICKMAN, D. L.; RALEIGH, E. L.; MOUSSEAU, T. A., 1995: Paternal investment in a seed beetle (Coleoptera: Bruchidae) influence of male size, age, and mating history. *Ann. Entomol. Soc. Am.*, **88**, 101–103.
- HANSEN, T. F.; PRICE, D. K., 1995: Good genes and old genes. Do old mates provide superior genes? *J. Evol. Biol.* **8**, 759–778.
- HEININGER, K., 2002: Aging is a deprivation syndrome driven by a germ–soma conflict. *Ageing Res. Rev.* **1**, 481–536.
- HEMPTINNE, J. -L.; DIXON, A. F. G.; ADAM, B., 2001: Do males and females of the two-spot ladybird, *Adalia bipunctata* (L.), differ in when they mature sexually. *J. Insect Behav.* **14**, 411–419.
- HODEK, I.; CERYNGIER, P., 2000: Sexual activity in Coccinellidae (Coleoptera): a review. *Eur. J. Entomol.* **97**, 449–456
- HODEK, I.; HONEK, A., 1996: *Ecology of Coccinellidae*. Dordrecht, Boston, London: Kluwer Academic Publishers, pp. 464.
- HODKOVA, M.; ZIEGLEROVA, J.; HODEK, I., 1991: Diapause in males of *Pyrhcoris apterous* and its dependence on photoperiod and activity of females of females. *Zool. Jb. Syst.* **118**, 279–285.
- ISOGAI, M.; SAKURAI, H.; TAKEDA, S., 1990: Relationship between spermatogenesis and diapause in the ladybird beetle, *Coccinella septempunctata brucki* Mulsant. *Res. Bull. Fac. Agric. Gifu University* **55**, 93–99.
- JONES, T. M.; BALMFORD, A.; QUINNELL, R. J., 2000: Adaptive female choice for middle-aged mates in a lekking sandfly. *Proc. R. Soc. Lond., B* **267**, 681–686
- KIRKPATRICK, M., 1987: Sexual selection by female choice in polygynous animals. *Ann. Rev. Ecol. Syst.* **18**, 43–70.
- KIRKWOOD, T. B. L., 2002: Evolution of ageing. *Mech. Ageing Develop.* **123**, 737–745
- KOKKO, H.; LINDSTROM, J., 1996: Evolution of female preference for old mates. *Proc. R. Soc. Lond., B* **263**, 1533–1538.
- MAJERUS, M. E. N., 1994: Female promiscuity maintains high fertility in ladybirds (Coleoptera: Coccinellidae). *Entomol. Mon. Mag.* **130**, 205–209.
- MANGEL, M., 2001: Complex adaptive systems, aging and longevity. *J. Theor. Biol.* **213**, 559–571.
- MANNING, J. T., 1985: Choosy females and correlates of male age. *J. Theor. Biol.* **116**, 349–354.
- MEDAWAR, P. B., 1946: Old age and natural death. *Modern Quart.* **2**, 30–49.
- MOORE, P. J.; MOORE, A. J., 2001: Reproductive ageing and mating: the ticking of the biological clock in female cockroaches. *Proc. Natl Acad. Sci., USA* **98**, 9171–9176.
- MORJAN, W. E.; OBRZYCKI, J. J.; KRASFUR, E. S., 1999: Inbreeding effects on *Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae). *Ann. Entomol. Soc. Am.* **92**, 260–268
- OBATA, S., 1987: Mating behaviour and sperm transfer in ladybeetle, *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae). *Appl. Ent. Zool.* **22**, 434–442.
- OBATA, S., 1988: Mating refusal and its significance in female of the ladybird beetle, *Harmonia axyridis*. *J. Physiol. Entomol.* **13**, 193–199.
- OBATA, S.; JOHKEI, Y., 1991: Comparative study on copulatory behaviour in four species of aphidophagous ladybirds. *Proceedings of 4th meeting of the IOBC W.G. Ecology of Aphidophaga*, 207–212.
- OMKAR; PERVEZ, A., 2002: Influence of temperature on the age-specific fecundity of a ladybird beetle, *Micraspis discolor* (Fabricius). *Insect Sci. Appl.* **22**, 61–65.
- OMKAR; SRIVASTAVA, S., 2002: The reproductive behaviour of an aphidophagous ladybird beetle, *Coccinella septempunctata* Linnaeus. *Eur. J. Entomol.* **99**, 465–470.
- PERVEZ, A., 2000: Contribution on prey-predator relationship and reproductive biology of a colour morph of *Propylea dissecta* (Mulsant) (Coccinellidae: Coleoptera). Ph.D. Thesis. Lucknow: University of Lucknow, pp. 197.
- PONSONBY, D. J.; COPLAND, M. J. W., 1998: Environmental influences on fecundity, egg viability and egg cannibalism in the scale insect predator, *Chilocorus nigrinus*. *BioControl* **43**, 39–52.
- PRIEST, N. K.; MACKOWIAK, B.; PROMISLOW, D. E. L., 2002: The role of parental age effects on the evolution of aging. *Evolution* **56**, 927–935.
- RICHARDS, A. M., 1980: Sexual selection, guarding and sexual conflict in a species of Coccinellidae (Coleoptera). *J. Aust. Entomol. Soc.* **19**, 26.
- ROBINE, J. M.; VAUPEL, J. W., 2001: Super centenarians, slower aging individuals or senile elderly? *Exp. Gerontol.* **36**, 915–930.
- ROTHSTEIN, M., 1982: *Biochemical Approches to Aging*. New York: Academic Press.
- SAVALLI, U. M.; FOX, C. W., 1998: Genetic variation paternal investment in a seed beetle. *Anim. Behav.* **56**, 953–961.
- SAVALLI, U. M.; FOX, C. W., 1999: The effect of male size, age, and mating behavior on sexual selection in the seed beetle *Callosobruchus maculatus*. *Ethol. Ecol. Evol.* **10**, 49–60.
- SAVALLI, U. M.; CZESAK, M. E.; FOX, C. W., 2000: Paternal investment in the seed beetle *Callosobruchus maculatus* (Coleoptera: Bruchidae): variation among populations. *Ann. Entomol. Soc. Am.* **93**, 1173–1178.
- SGRO, C. M.; PARTRIDGE, L., 1999: A delayed wave of death from reproduction in *Drosophila*. *Science* **286**, 2521–2524.
- THORNHILL, R.; ALCOCK, J., 1983: *The Evolution of Insect Mating Systems*. Cambridge, MA: Harvard University Press.
- TREGENZA, T.; WEDELL, N.; HOSKEN, D. J.; WARD, P., 2003: Maternal effects on offspring depend on female mating pattern and offspring environment in yellow dung flies. *Evolution* **57**, 297–304.
- TRIVERS, R. L., 1972: Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man – 1871–1971*. Ed. by CAMPBELL, B. Chicago, IL: Aldine Press, 136–179.

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