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Parental age at mating affects reproductive attributes of the aphidophagous ladybird beetle, *Coelophora saucia* (Coleoptera: Coccinellidae)

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Abstract. Ageing and its affect on life attributes have not been widely explored in ladybirds. The present study investigates the influence of female and male age at mating on the reproductive attributes of the ladybird beetle, *Coelophora saucia* (Mulsant). All reproductive attributes, viz. fecundity, percentage egg hatch, pre-oviposition, oviposition and post-oviposition periods were found to be influenced by the ages of both females and males at mating. This is unlike the results of previous studies on ladybirds, where male age was found to influence only percentage egg hatch. The influence of male age at mating on fecundity and reproductive periods is probably due to age influenced variation in seminal proteins, which influence fecundity and when the eggs are laid.

INTRODUCTION

Senescence can be defined demographically as an age-dependent increase in mortality risk, or functionally as a decline in performance (Medawar, 1952; Williams, 1957; Rose, 1991; Partridge & Gems, 2002), and can be accounted for by several evolutionary and mechanistic theories (see Hughes & Reynolds, 2005). The understanding of the ageing process is based on the relationship between the demographic and functional aspects, which are believed to be tightly linked, as ageing involves a decline in performance of several body functions, leading to increased mortality (Williams, 1999), and is observed in organisms ranging from flies (Grotewiel et al., 2005) to human beings (Burke & Barnes, 2006).

This decline in physiological performance with age is known to be influenced by a number of factors prominent amongst which are dietary restrictions (Piper & Partridge, 2007 and references therein) and reproduction (Rose, 1984; Finch, 1990, 1998; Tatar et al., 1993; Partridge et al., 1999; Finch & Ruvkun, 2001; Robine, 2001). The acceleration of ageing in reproductively active individuals (Arnqvist & Nilsson, 2000; Priest et al., 2002; Mishra & Omkar, 2006), which is reflected in a deterioration in fitness and increase in mortality rate, is reported for a number of insects (Rose, 1984; Van Voorhies, 1992; Simmons & Bradley, 1997; Mishra & Omkar, 2006). The mechanism is explained in terms of reproductive costs (Partridge, 1986; Omkar & Mishra, 2005) and trade offs (Kokko, 1998; Finch & Ruvkun, 2001; Robine, 2001; Mishra & Omkar, 2006).

Ageing is likely to affect mate choice and mortality patterns (Hansen & Price, 1995; Kokko, 1998; Beck & Powell, 2000; Kindlmann et al., 2001; Dixon & Agarwala, 2002; Mishra & Omkar, 2006). Although ageing has considerable implications for individual fitness, even in wild populations (Nesse, 1988; Bonduriansky & Brassil, 2002), studies have typically relied on aggregate statistics from cohorts, while individual and sex specific variation in ageing rates remain poorly understood (Austad, 1996; Service et al., 1998; Partridge & Mangel, 1999; Zens & Peart, 2003; Mishra & Omkar, 2006). Priest et al. (2002) recorded the role of sex-specific ageing on the fitness and survival patterns of future generations; maternal age and to a lesser extent paternal age were found to have a large influence on offspring longevity and their age-specific mortality. This aspect however needs further study.

As ageing is the outcome of inherent life-history trade offs and the condition of organisms, its effects can be recorded by changes in a number of aspects, such as fecundity, egg hatch and mortality, which have been exhaustively studied in many insects (Williams, 1957; Hamilton, 1966; Kirkwood, 1977; Partridge & Barton, 1993). Recent studies on arthropods have investigated the effect of male or female age on mate choice (Hansen & Price, 1995; Kokko, 1998; Beck & Powell, 2000; Proulx et al., 2002), sperm quality and quantity (Hayashi, 1999; Green, 2003) sperm transfer rates (Jones et al., 2006), last male sperm precedence (LaMunyon, 2001; Schafer & Uhl, 2002; Mack et al., 2003; Radwan et al., 2005), sperm competitive ability (Service & Fales, 1993; Jones et al., 2006), musculature of genital tract (Mack et al., 2002) and sperm storage (Taylor et al., 2001). However, the very basic influence of age on life attributes is yet to be explored in detail in ladybirds, for which there are only a few studies (Dixon & Agarwala, 2002; Pervez et al., 2004; Srivastava & Omkar, 2004; Mishra & Omkar, 2004, 2006; Omkar & Singh, 2005; Omkar et al., 2006; Omkar & Mishra, 2009). While most of these studies have concentrated on the effect of age on various reproductive parameters, the results are dependent on the species studied and require further study. The age at mating is an interesting aspect of age related studies in ladybirds.

Coelophora saucia (Mulsant), commonly called the Macular site ladybug and the Tokyo star in China, is an aphidophagous ladybird beetle, which is common in Northern India, China, Japan, Tawain, Thailand, Indonesia, Malaysia, Philippines, Vietnam and Korea (Hirano et al., 1996; Han, 1997; Berg et al., 1997; Omkar et al., 2005; Singh & Tripathi, 2008). It is a relatively little studied ladybird, with only a few studies on its life attributes (Omkar & Pathak, 2006, 2007; Omkar et al., 2005; Pathak, 2008) and none on the effect of parental age at mating. The present study investigates the effect of parental age at mating on reproductive attributes of *C. saucia* and increases the level of knowledge on this beetle and of ladybird physiology in general.

MATERIAL AND METHODS

Stock culture

Adults of *C. saucia* were collected from colonies of the aphid, *Aphis craccivora* Koch infesting bean (*Dolichos lablab* Linnaeus) in fields around Lucknow and brought to the laboratory (25 ± 2°C, 60 ± 5% R.H and 14L: 10D). They were paired and reared in Petri dishes (9.0 × 2.0 cm) on an *ad libitum* supply of prey (same species of aphid as above). Eggs were collected daily and the larvae reared to the pupal stage in glass beakers (11.0 × 9.0 cm) in which the aphid prey was replenished daily. Beakers containing pupae were observed twice a day and newly emerged (NE) adults were sexed and isolated in Petri dishes and provided with an ad libitum supply of *A. craccivora*, which was replenished daily.

Experimental setup

(A) Effect of female age

Unmated adults of requisite ages were obtained from the stock culture. Virgin females aged 0 (newly emerged: NE), 1, 2, 4, 6, 8, 10, 20, 30, 40, 50 and 60 days were paired once with 10-day-old males in plastic Petri dishes (9.0 × 2.0 cm). Thereafter, the females were isolated and reared on a daily replenished ad libitum supply of *A. craccivora* for the remainder of their life. Number of eggs laid and subsequent percentage egg hatch were recorded daily. All observations were made once every 24 h. There were 10 pairs in each mating group (n = 10).

(B) Effect of male age

Unmated adults of requisite ages were obtained from the stock culture. Virgin males aged 0 (newly emerged: NE), 1, 2, 4, 6, 8, 10, 20, 30, 40, 50 and 60 days were paired once with 10-day-old females in plastic Petri dishes (9.0 × 2.0 cm). Thereafter, the females were isolated and reared on a daily replenished ad libitum supply of *A. craccivora* for the remainder of their life. Number of eggs laid and percentage egg hatch were recorded once every 24 h. As above there were 10 pairs in each mating group.

Statistical analysis

Data were checked for normality and found to be normally distributed. All percentages were arcsine square root transformed prior to statistical analysis. Data on pre-oviposition (time between mating and start of oviposition), oviposition (time spent egg laying) and post-oviposition (time between cessation of egg laying and death of females) periods, fecundity and percentage egg hatch were subjected to one-way ANOVA followed by post hoc Tukey's honest significance test using statistical software MINITAB (Minitab, 2000) with female or male age as the varying factor. Reproductive rate (fecundity/oviposition period) was also calculated and subjected to ANOVA. Data on NE to 4 day-old males, which did not mate, were not included in the analysis. Fecundity and percentage egg hatch were regressed against both female and male age in order to determine the relationships between these two parameters and age.

RESULTS

(A) Effect of female age

Females in all the age groups mated. Females of *C. saucia* that mated at the age of 20 days laid most eggs (1979.6 ± 197.9; Mean ± SE) and those mated when 60 days old the least (240.0 ± 16.3) (Table 1). Fecundity differed significantly with the age at mating of females (F = 85.09; P < 0.001; d.f. = 11,119; Table 1) and showed a parabolic trend ($Y = –35.053X^2 + 484.64X – 419.65$; $r^2 = 0.5815$; Fig. 1) with a peak at female age of 20 days. Percentage egg hatch was also found to differ with age at mating of females, albeit less significantly (F = 6.23; P < 0.01; d.f. = 11,119; Table 1). It was highest for females

TABLE 1. Influence of female age at mating on the reproductive parameters of *C. saucia.*

Female age at time of mating	Fecundity (no. of eggs)	Percentage egg hatch	Pre-oviposition period (in days)	Oviposition period (in days)	Post oviposition period (in days)	Longevity (in days)	Reproductive rate
NE	393.1±13.3b	71.9±2.5a	6.5±0.6e	27.8±0.9c	27.2±2.1f	54.0±4.6b	14.1±0.2a
1	447.6±23.0c	80.7±1.2b	6.2±0.3e	28.2±0.7c	15.4±2.6e	45.3±4.2a	15.9±0.9b
2	508.3±15.5c	81.2±3.2b	5.3±0.4d	29.5±1.5c	14.9±1.8e	46.9±3.5a	17.6±0.8b
4	606.5±19.3d	83.4±1.8b	4.2±0.4c	30.7±1.3c	14.2±2.2e	50.5±3.8ab	19.9±0.5b
6	647.2±34.3d	88.1±1.1	3.9±0.2c	35.3±1.7d	8.3±1.5bc	51.1±3.9ab	18.4±0.7b
8	1121.1±82.1f	89.6±1.2c	2.9±0.3bc	38.5±2.8d	9.3±2.5c	51.3±4.1ab	30.5±3.1d
10	1506.4±150.6h	91.5±9.1cd	2.1±0.2bc	49.4±4.9e	5.9±0.6a	63.4±6.3c	27.9±2.8c
20	1979.6±197.9i	93.2±9.3d	1.3±0.1b	56.0±5.6e	7.8±0.8b	65.1±6.5c	35.6±3.6d
30	1219.7±102.9g	89.9±5.4c	2.0±0.2bc	36.9±2.3d	7.4±1.0b	65.5±0.9c	33.9±3.6d
40	853.8±46.2e	82.7±3.8b	0.3±0.2a	27.7±2.4c	4.2±0.7a	64.9±0.6c	32.5±2.9d
50	458.4±30.2b	76.7±4.3a	0.0±0.0a	20.4±2.3b	12.0±0.1d	73.1±0.4d	24.8±3.1c
60	240.0±16.3a	72.7±3.5a	0.0±0.0a	12.7±1.4a	6.7±0.5b	72.7±3.5d	20.8±2.7b
F-value	85.09**	6.23*	60.08**	43.55**	13.22**	10.87**	12.00**

Values are Mean ± S.E. * and ** indicate F-values significant at P < 0.01 and P < 0.001, respectively. Values in a column followed by different letters are significantly different.

TABLE 2. Influence of male age at mating on the reproductive parameters of *C. saucia*.

Male age at time of mating	Fecundity (no. of eggs)	Percentage egg hatch	Pre-oviposition period (in days)	Oviposition period (in days)	Post-oviposition period (in days)	Longevity (in days)	Reproductive rate
NE	–	–	–	–	–	–	–
1	–	–	–	–	–	–	–
2	–	–	–	–	–	–	–
4	–	–	–	–	–	–	–
6	433.6±43.4a	84.4±8.4a	4.3±0.4c	20.7±2.1a	17.3±1.7d	51.1±5.1a	21.7±2.2a
8	673.0±67.3b	88.1±8.8a	3.8±0.4	31.0±3.1b	13.6±1.4c	47.3±4.7a	21.7±2.2a
10	1506.4±150.7d	91.5±9.2ab	2.1±0.2a	49.4±4.9d	5.9±0.6b	63.4±6.3a	27.9±2.8b
20	1653.3±165.3d	92.8±9.3b	2.8±0.3ab	38.4±3.8c	1.5±1.0a	55.0±5.5a	43.7±4.4c
30	1724.0±172.4d	94.7±9.5b	2.2±0.2a	39.2±3.9c	11.2±1.1c	60.5±6.1a	45.4±4.5c
40	904.0±90.4c	90.3±9.0ab	3.0±0.3b	32.9±3.3b	17.7±1.7d	63.7±6.4a	27.9±2.8b
50	696.5±69.6b	87.7±8.8a	2.3±0.2a	30.2±3.0b	17.4±1.7d	60.6±6.1a	23.9±2.4a
60	534.3±53.4a	81.4±8.1a	3.2±0.3ab	24.4±2.0a	20.4±2.0e	56.5±53.4a	22.1±2.2a
F-value	49.82**	4.17*	7.27**	35.73**	7.01**	7.11**	13.84**

Values are Mean ± S.E. * and ** indicate F-values significant at $P < 0.01$ and $P < 0.001$, respectively. Values in a column followed by different letters are significantly different.

mated when 20 days old (93.2 ± 9.3%) and lowest for females mated at 60 days of age (72.7 ± 3.5%) ($Y = -0.6211X^2 + 8.1866X + 63.917$; $r^2 = 0.9118$; Fig. 1). The reproductive periods, viz. pre-oviposition ($F = 60.08$; $P < 0.001$; d.f. = 11,119), oviposition ($F = 43.55$; $P < 0.001$; d.f. = 11,119) and post-oviposition ($F = 13.22$; $P < 0.001$; d.f. = 11,119) also differed significantly for the females mated at different ages. Pre-oviposition period decreased with increase in female age at mating up to 20 days and then increased, with a reverse trend in the oviposition period. Post-oviposition period on the other hand decreased with increase in female age at mating up to 40 days and then increased. The reproductive rate showed a parabolic relationship with female age at mating ($F = 13.84$; $P < 0.001$; d.f. = 11,119; Table 1) with the peak at 20 days. Longevity increased with female age at mating. Thus, female age at mating significantly affected all the reproductive parameters, viz. pre-oviposition, oviposition and post-oviposition periods, fecundity and percentage egg hatch.

(B) Effect of male age

Recently emerged to 4 day old males did not mate and thus no reproductive parameters were recorded for them. In all the other treatments the males mated with females. The pre-oviposition period of female *C. saucia* mated with males of different ages differed significantly ($F = 7.27$; $P < 0.001$; d.f. = 7,79; Table 2), as did the oviposition ($F = 35.73$; $P < 0.001$; d.f. = 7,79; Table 2) and post-oviposition periods ($F = 7.11$; $P < 0.001$; d.f. = 7,79; Table 2). Fecundity also differed significantly with male age at mating ($F = 49.82$; $P < 0.001$; d.f. = 7,79; Table 2) with those females mated to males aged 30 days having the highest fecundity. However, there was no significant difference in the fecundity of females that were mated with 10-, 20- or 30-day old males. Fecundity in *C. saucia* increased with the age of the males that were mated with up to the age of 30 days, after which it declined ($Y = -95.077X2 + 844.81X - 361.54$ $r^2 = 0.7808$; Fig. 2). Percentage egg hatch was also influenced by paternal age at mating ($F = 4.17$; $P < 0.01$; d.f. = 7,79; Table 2) and was highest when males were 30 days old ($Y = -0.8698X^2 +$

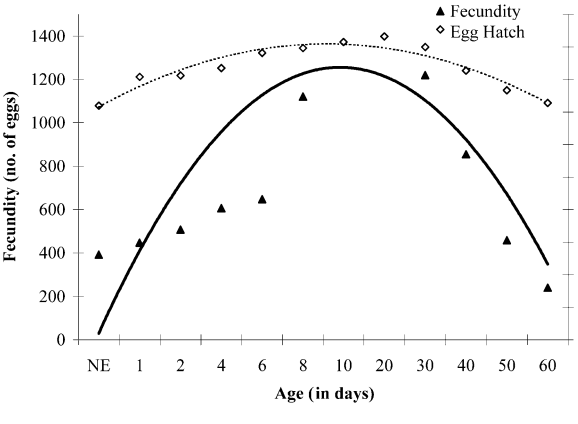

Fig. 1. The relationships between female age at mating, fecundity and egg hatch in *C. saucia*. Bold line indicates the trend in fecundity and the dashed line the trend in percentage egg hatch.

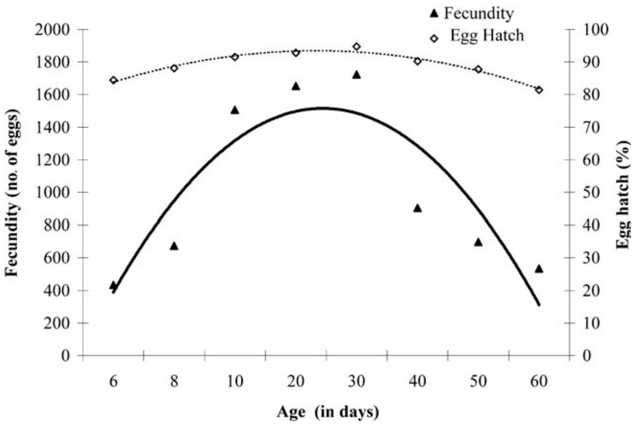

Fig. 2. The relationships between male age at mating, fecundity and egg hatch in *C. saucia*. Bold line indicates the trend in fecundity and the dashed line the trend in percentage egg hatch.

7.5392X + 77.123; $r^2 = 0.964$; Fig. 2). The reproductive rate was also significantly dependent on male age at mating ($F = 13.84$; $P < 0.001$; d.f. = 7,79; Table 2). It was highest when the females were mated with 30 day old males, but not statistically different from when mated with 20 day old males.

DISCUSSION

The results reveal that the ages of both the female and male at mating affect reproductive performance in *C. saucia.* All reproductive parameters, viz. pre-oviposition, oviposition and post-oviposition periods, fecundity, percentage egg hatch and reproductive rate, were influenced by the ages of both the female and male at mating. An effect of the age of both sexes at mating on all reproductive parameters has not been reported before in ladybirds. Previous studies on ladybirds, viz. *Propylea dissecta* (Mulsant), *Cheilomenes sexmaculata* (Fabricius), and *Coccinella septempunctata* Linnaeus revealed the effect of male age is limited to percentage egg hatch and had no effect on fecundity and the length of the reproductive period (Pervez et al., 2004; Srivastava & Omkar, 2004; Mishra & Omkar, 2004; Omkar et al., 2006).

Fecundity in *C. saucia* was greatest when the females were first mated at the age of 20 days and for 10 day old females mated with 30 day old males. In another ladybeetle, *Cryptolaemus montrouzieri* Mulsant, 5–15 day old females laid the highest number of eggs (Jalali et al., 1999) and 20-day-old females of *C. septempunctata* and the pale morph of *P. dissecta* are the most fecund (Pervez et al., 2004; Srivastava & Omkar, 2004). However, 30-day-old females of the typical morph of *P. dissecta* are the most fecund (Mishra & Omkar, 2004). Begon & Parker (1986) previously suggested that egg or clutch size should change with maternal age, and this is recorded in a number of butterflies (Jones et al., 1982; Murphy et al., 1983; Wiklund & Persson, 1983; Karlsson & Wiklund, 1984, 1985). In ladybirds, the constraint on egg size (Dixon & Guo, 1993) indicates that the variation in fecundity is a result of a change in clutch size. Since in ladybirds, the clutch size is half the number of ovarioles (Stewart et al., 1991) it is likely that the number of mature ovarioles decreases with age, which needs to be verified.

The decline in percentage egg hatch with maternal age indicates there are changes in the physiological state of the female genital tract, which might influence sperm transfer and motility. In *Drosophila melanogaster* mating with females older than 17 days, significantly reduced the precedence of the last male's sperm, indicating the outcome of sperm competition to be dependent on the physiological condition of the female genital tract (Mack et al., 2002). They suggest that the ability of the seminal receptacle to receive sperm from a new mating might be reduced because of functional senescence.

The decline in fecundity/egg hatch/reproductive output of older females might also be due to a preference for mating with older males. Genetic benefits of selecting partners are grouped into the two well recognized categories: "good genes" and "sexy sons" (Andersson, 1994). The recently added third kind of benefit is the production of genetically fit offspring by selecting genetically compatible mates (Zeh & Zeh, 1996, 1997, 2003; Tregenza & Wedell, 2000), which is influenced by the accumulation of mutations and activation of late acting pleiotropic genes with increase in age (Partridge & Barton, 1993; Pletcher & Curstinger, 1998). It is thus likely that in the present study in which females of all ages were mated with young males (10 days old), the accumulation of mutations and activation of pleiotropic genes in older females might have reduced their fecundity. Also, the males might manipulate their ejaculate size in accordance with the age of females and so cause a decline in their reproductive output. Female age may also influence the probability of copulation or subsequent patterns of fertilization as is reported for the oblique-banded leaf roller *Choristoneura rosaceana* (Harris), where the former declines with age (Delisle, 1995) and possibly influences egg hatch.

The results also reveal that male age influenced all the reproductive parameters in *C. saucia*, not only egg hatch as in other ladybirds (Pervez et al., 2004; Srivastava & Omkar, 2004; Mishra & Omkar, 2004; Omkar et al., 2006). Such an influence on fecundity and reproductive period is recorded for species in which the males provide the females with nutrients during copulation (Fox, 1993a, b; Fox et al., 1995a; Savalli & Fox, 1999a, b; Savalli et al., 2000). That this may occur in *C. saucia* is indicated by the increase in the longevity of females that mate many times compared with those that only mated once or a few times, as is recorded in another publication on this beetle (Omkar et al., 2010). Nutritional inputs provided by males are reported to take the form of (a) gifts of food (Arnqvist & Nilsson, 2000) and/or (b) by varying the quantity and quality of the ejaculates (Arnqvist & Nilsson, 2000). The former practice has not been observed in *C. saucia*, so the latter is likely to play a role in the change in reproductive parameters of females mated with males of different ages. A study by Fox et al. (1995b) on *C. maculatus* revealed a change in the quantity and quality of the ejaculate with age. Gillot (2003) reviewed the effect of male age on the quality and concentration of proteins in semen that are known to influence female fecundity and time of oviposition. Change in the frequency with which females mate along with male age might also determine the change in reproductive parameters (Fox et al., 1995b). A reduction in the quantity of sperm transferred with increase in male age may also account for the reduced fecundity of females.

The influence of paternal age on percentage egg hatch is reported for ladybirds (Pervez et al., 2004; Srivastava & Omkar, 2004). This is most likely a consequence of age related changes in the physiological state of males.. This might manifest itself in four ways (a) sexual maturity of male (Pitnick et al., 1995; Baker et al., 2003), (b) change in quality or quantity of sperm with age (Hayashi, 1999; Taylor et al., 2001; Green, 2003) , (c) change in the ability to transfer sperm (Jones et al., 2006), and/ or (d) change in sperm precedence and competitive ability

(LaMunyon, 2001; Schafer & Uhl, 2002; Mack et al., 2003; Radwan et al., 2005; Jones et al., 2006). In the hide beetle, *Dermestes maculatus* DeGeer, the probability of sperm transfer and the amount of sperm transferred vary with male age, but not with female age. Middle aged and old males are more likely to transfer sperm successfully and a greater quantity of sperm than young males. Sperm competitive ability varies with middle aged males achieving greater fertilization success when competing with young or old males (Jones et al., 2006).

The results of the present study may also indicate mate choice in *C. saucia*. Mate choice models for insects reveal that in certain cases young males have a selective advantage over older males (Hansen & Price, 1995). The possible reason for this is their better genetic constitution (fewer mutations and lower pleiotropic activity of late acting genes; Partridge & Barton, 1993; Pletcher & Curstinger, 1998). The high reproductive output of the females mated with 10 to 30-day-old males may indicate males in that age range are likely to be the preferred mates. This needs to be tested experimentally by age-based studies on mate choice in which the fitness consequences are recorded.

Thus, the present study reveals that both male and female age at mating altered the reproductive parameters, with the 20-day-old females mated with 10 to 30-day-old males being the most productive.

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