EUROPEAN JOURNAL OF ENTOMOLOGY
ISSN (online): 1802-8829
http://www.eje.cz
Eur. J. Entomol. **113**: 44–50, 2016
doi: 10.14411/eje.2016.005
ORIGINAL ARTICLE

Mating alters the rate of development of ovarioles in the ladybird, *Propylea dissecta* (Coleoptera: Coccinellidae)

Mhd SHAHID, Arshi SIDDIQUI, OMKAR and Geetanjali MISHRA*

Ladybird Research Laboratory, Department of Zoology, University of Lucknow, Lucknow-226007, India;
e-mails: geetanjalimishra@hotmail.com, shahidgr786@mil.com, arshi.apda@gmail.com, omkaar55@hotmail.com

Key words. Coleoptera, Coccinellidae, *Propylea dissecta*, age, mating status, ovariole development, egg maturation, egg load

Abstract. The influence of female mating status on ovarian development of the ladybird, *Propylea dissecta* (Mulsant) (Coleoptera: Coccinellidae), was investigated under laboratory conditions. We assessed the extent to which ovariole development was affected by mating and for that we initially created a base line by observing age specific ovariole development. Results show that the number of follicles in each ovariole increased with the age of both virgin and mated females up to the age of 3 days, thereafter, no increase in number of follicles was recorded. Ovariole width also increased with age in both virgin and mated females up to 4 days, thereafter, no increase in ovariole width was recorded. The ovariole width of mated females was significantly greater than that of virgin females. Egg maturation and the egg load started to increase at the age of 8 days in virgin females. Thereafter, it increased with increase in female age. While in mated females, immature eggs were recorded in their ovarioles from the age of 1 to 2 days. In mated females, however, the increase in the number of mature eggs per ovariole and egg load started when they were 3 days old. Egg load continuously increased with increasing female age.

INTRODUCTION

Ovarian development, a highly dynamic process (see review by Papaj, 2000), has been investigated extensively in insects, such as, fruit flies (Begun et al., 2006; Findlay et al., 2008), beetles (Kawazu et al., 2011, 2012; Ryall et al., 2013) and ladybird beetles (Hodek & Ceryngier, 2000; Ceryngier et al., 2004; Hodek, 2011; Nedved & Honek, 2011; Choate & Lundgren, 2013). Oocytes develop within ovarioles, arising from stem cells in the terminal filament and form a follicle along with trophocytes or nurse cells (Heming, 2003). The nurse cells act as a source and transport mechanism for vitellogenesis; sequestering, synthesizing compounds and delivering them to the growing oocytes via specialized channels. In advanced stages, mature oocytes can often be seen within each ovariole (Buning, 1994). A five-stage rating system has been proposed to describe ovarian development in insects based on the length of the terminal follicle, the number and shape of follicles developing in each ovariole and presence of yellow yolk in the terminal oocyte (Jarvis & Copland, 1996).

The maturation of ovaries in females is normally correlated with age, until sexual maturity is reached (Adams, 2000; Brent, 2010). However, factors other than age, such as food consumption (Papaj, 2000), temperature (Atlihan & Chi, 2008; Wang et al., 2013), photoperiod (Wang et al., 2013) and social interactions (Uzsak & Schal, 2012, 2013), have a major role in influencing the rate of sexual maturation. In tephritid fruit flies, rate of ovarian maturation increases with increase in the availability of food (Papaj, 2000) and is sometimes delayed by a lack of protein in their diet (Blay & Yuval, 1999).

Other than the above mentioned factors influencing ovariole maturation, mating also acts as an accelerating factor (Jin & Gong, 2001; Uchida et al., 2003; Horton et al., 2005). A number of biologically active compounds, such as seminal fluid proteins, fecundity-enhancing substances (FES), sex peptides (SP) and ovulin, present in seminal fluid probably trigger important behavioural, morphological, and functional transformations essential to support the reproductive success of inseminated females (Gillott & Friedel, 1977; Avila et al., 2011).

In insects, seminal fluid proteins (SFP) are primarily produced in the male accessory gland and are generally referred to as accessory gland proteins (AGPs) (Walters & Harrison, 2008, 2010; Baer et al., 2009). A wide repertoire of AGPs are recorded in a number of insects, including fruit flies (Mueller et al., 2005; Wagstaff & Begun, 2005; Walker et al., 2006), butterflies (Walters & Harrison,

* Corresponding author.

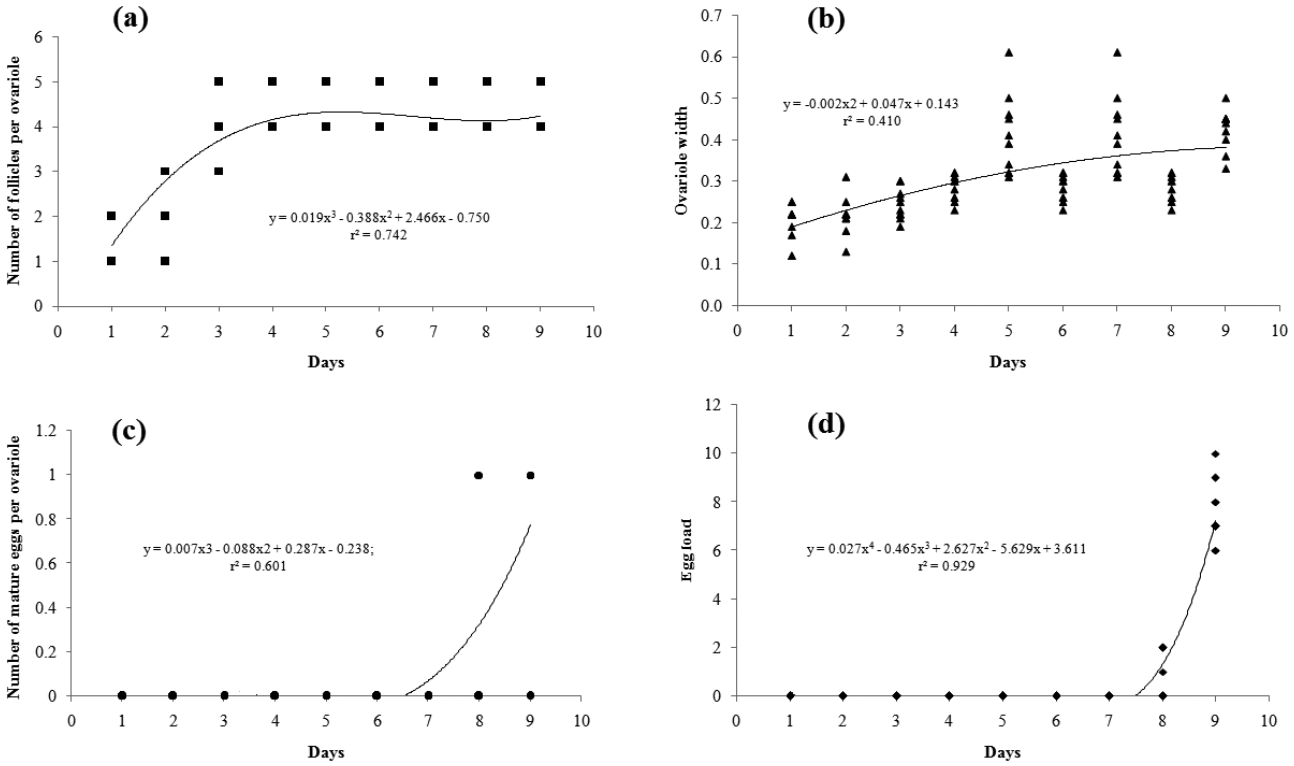

Fig. 1. The number of follicles per ovariole (a), ovariole width (b), number of mature eggs per ovariole (c) and egg load (d), recorded for virgin females of different ages of *P. dissecta*.

2008, 2010) and crickets (Andres et al., 2006; Braswell et al., 2006). AGPs in insects enhance fecundity (Gillott & Friedel, 1977; Gillott, 2003; Yamane et al., 2015) and act as oviposition stimulants (Simmons, 2011). Sex peptides (Chen et al., 1988; Chapman et al., 2003; Liu & Kubli, 2003) and ovulin (Herndon & Wolfner, 1995; Heifetz et al., 2000, 2005) are known to stimulate egg laying in mated females.

In ladybirds, little work has been done on ovariole development and the factors affecting it, including the role of AGPs. The few studies on ovariole development in ladybirds indicate that the number of ovarioles is species specific and dependent on the environment of developing larvae (see Hodek et al., 2011). Ferrer et al. (2008) report a negative effect of suboptimal larval diet on ovariole number in *A. bipunctata* but the opposite trend was recorded in similar experiments on *H. axyridis* and a different population of *A. bipunctata* (Ware et al., 2008). Starvation also does not result in *Harmonia axyridis* developing fewer ovarioles but in a reduction in the percentage of mature ovarioles (Osawa, 2005).

The evidence linking ovariole development with age is contradictory and little is known about the underlying mechanisms of ovariole development in ladybirds. We, therefore, chose to investigate the normal ovariole development with increase in age and effect of mating on this phenomenon in the polyphagous ladybird beetle, *Propylea dissecta*. *P. dissecta* is small and has three morphs: pale, intermediate and typical (the pale and typical being most common). The male and female can be easily differentiated on the basis of patches present on the head and pronotum (Omkar & Pervez, 2000, 2005). It feeds voraciously on the colonies of aphids, viz. *Aphis gossypii* (Glover) and *Aphis craccivora* (Koch), infesting *Lagenaria vulgaris* Seringe and *Dolichos lablab* L., respectively (Omkar & Mishra, 2005).

MATERIAL AND METHODS

Stock maintenance

Adults of *P. dissecta* (twenty five pairs) were collected from aphid infested agricultural crops in fields surrounding Lucknow (26°50′N, 80°54′E), U.P., India. They were paired and kept in transparent plastic Petri dishes (9.0 × 2.0 cm) under standard laboratory conditions (27 ± 1°C; 65 ± 5% R.H.; 14L : 10D photoperiod) and provided with an ad libitum supply of *Aphis craccivora* Koch (Hemiptera: Aphididae) (infested stems of cowpea, *Vigna unguiculata* L., reared in a glasshouse at 28 ± 1°C, 65 ± 5% R.H.). The eggs laid by this ladybird were placed in an environmental test chamber (Yorco Super Deluxe, YSI-440, New Delhi, India) until they hatched. The larvae were reared in plastic beakers (15.0 × 12.0 cm; 5 larvae per beaker) and provided an abundant supply of *A. craccivora* infested on cowpea twigs, which was replenished daily. The newly emerged adults were isolated and placed individually in Petri dishes (size as above) and thereafter used for experimental purposes. Beetles collected in the field were added from time to time to the laboratory culture in order to avoid inbreeding.

Experimental design

(A) Base line of ovariole development (effect of age)

Newly emerged unmated females were taken from the stock culture and placed individually in plastic Petri dishes (9.0 × 2.0 cm) until they reached the required age; one of ten age groups – 0 (6-h), 1, 2, 3, 4, 5, 6, 7, 8 and 9 days – with 10 females per age group (n = 10). On reaching the requisite ages, the females were killed with the help of cotton wool soaked in diethyl ether ($C_4H_{10}O$, M = 74.12 g/

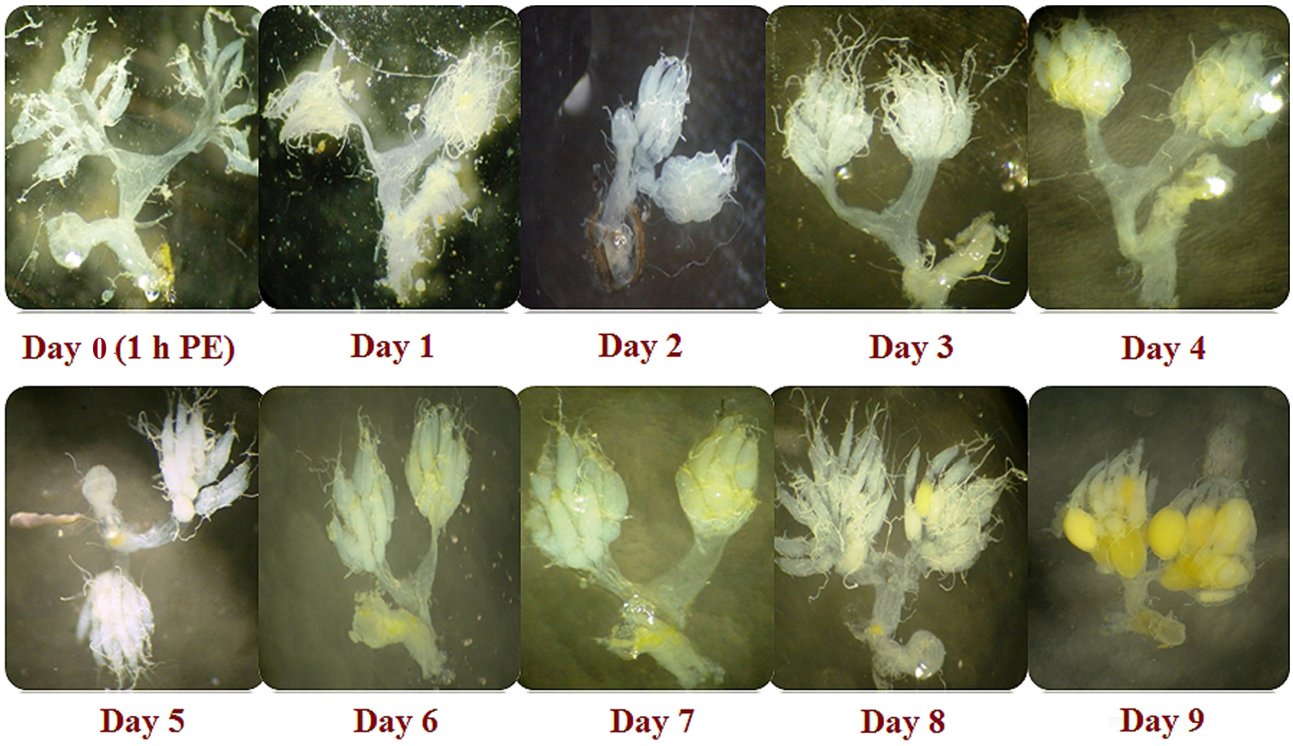

Fig. 2. Age specific ovariole development in virgin *P. dissecta* female. PE stands for post emergence.

mol). These females were carefully dissected and the ovaries along with oviduct and common oviduct were removed and placed on a slide in a few drops of saline. These were then observed under a stereoscopic binocular microscope (Magnus, Olympus India, Noida) at 16× magnification. Number of follicles per ovariole, ovariole width, number of mature eggs per ovariole and egg load (total number of mature eggs in an ovary) were recorded (following Jarvis & Copland, 1996).

(B) Effect of mating on ovariole development

This study was designed to investigate the effect of mating on ovariole development in ladybirds. For this purpose, a newly emerged 0-day-old (6 h post emergence) female was placed with a 10-day-old sexually mature unmated male in a Petri dish (9.0 × 2.0 cm). Females took 19.22 ± 1.30 min to establish mating and mated for 3.42 ± 0.14 h. Females showed resistance to being mated by rolling in her abdomen, kicking with her legs and moving fast, but the males managed to establish genital contact in all cases. After completion of mating, the male was removed and the female was isolated along with abundant *A. craccivora*. The Petri dishes were placed in an environmental test chamber (abiotic conditions similar to stock) for 24 h. After 24 h (i.e. at the age of 1 day), the mated female was killed and carefully dissected (as above). Similarly, 1, 2, 3 and 4-day-old females were mated with 10-day-old sexually mature unmated males and killed 24 h post mating, i.e. at the ages of 2, 3, 4 and 5 days, respectively. Virgin females of the same age as that of the mated females (at time of dissection) were also dissected and their reproductive systems measured as a control. The same measurements were recorded as in section (A). The observations were made on ten females (n = 10) per treatment.

Statistical analysis

Data obtained in experiment (A) on the number of follicles in each ovariole, ovariole width, number of mature eggs per ovariole, and egg load recorded for females of different ages (0, 1, 2, 3, 4, 5, 6, 7, 8 and 9 days) were subjected to polynomial regression analysis. To determine the effects of mating (Experiment B) on ovariole maturation, the number of follicles in each ovariole, ovariole width, number of mature eggs per ovariole and egg load were analyzed using two-way ANOVA followed by post hoc Tukey's test with female age (1, 2, 3 and 4 days) and mating status (mated and virgin females) as independent factors. All analyses were carried out using MINITAB 16 statistical software (Minitab Inc., State College, Pennsylvania, USA).

RESULTS

(A) Base line of ovariole development

The number of follicles in each ovariole increased significantly with increasing female age, up to three days of age ($y = 0.019x^3 – 0.388x^2 + 2.466x – 0.750$; $R^2 = 0.742$; $P < 0.01$; Fig. 1a). The ovariole width also significantly increased with increase in female age, up to four days of age ($y = –0.002x^2 + 0.047x + 0.143$; $R^2 = 0.410$; $P < 0.01$; Fig. 1b).

The number of mature eggs per ovariole significantly increased with female age ($y = 0.007x^3 – 0.088x^2 + 0.287x – 0.238$; $R^2 = 0.601$; $P < 0.01$; Fig. 1c). Between 1 to 7 days, only immature eggs were recorded in the ovarioles. Mature eggs were first recorded on day 8 in virgin females, followed by a rapid increase with increasing female age (Fig. 2).

Egg load significantly increased with female age as depicted by the quadratic regression equation ($y = 0.027x^4 – 0.465x^3 + 2.627x^2 – 5.629x + 3.611$; $R^2 = 0.929$; $P < 0.001$; Fig. 1d). Mature eggs were first recorded in 8 day old females and then increased with age (Fig. 2).

(B) Effect of mating on ovariole development

The results of two-way ANOVA revealed that the number of follicles in each ovariole was affected by both fe-

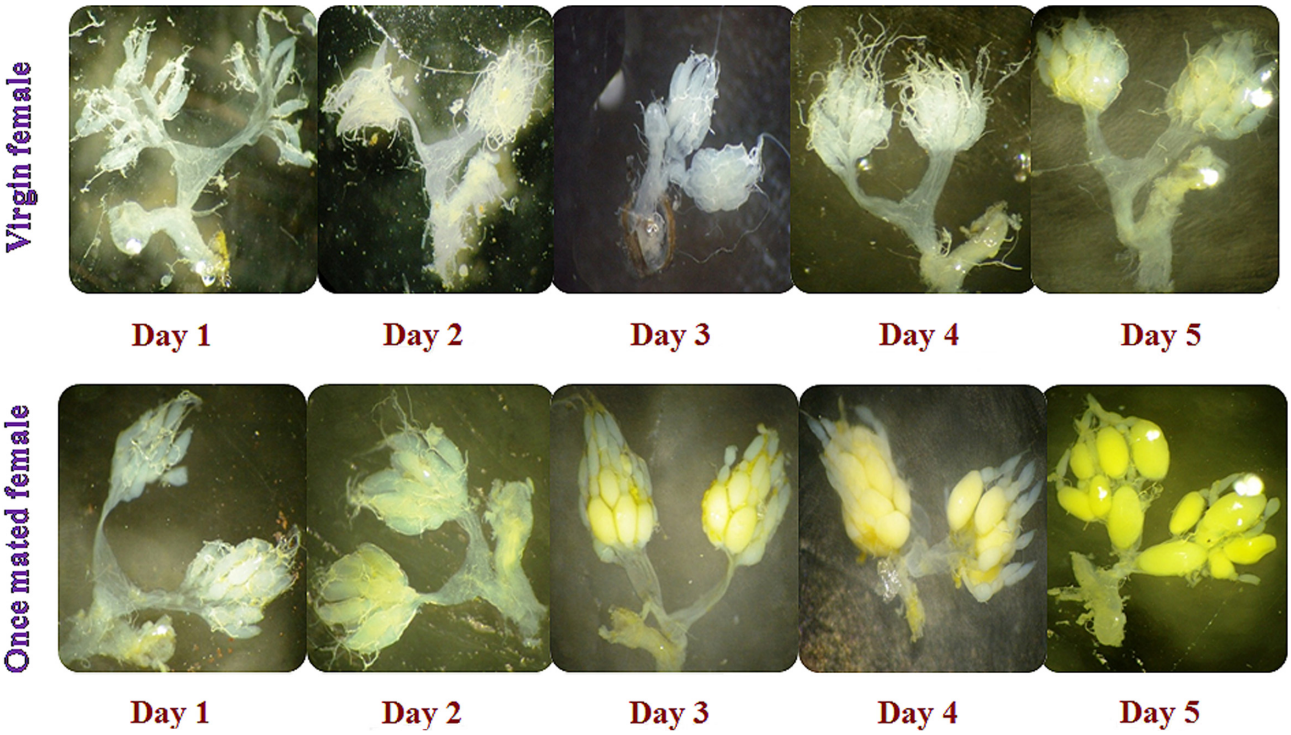

Fig. 3. Effect of mating on ovariole development in *P. dissecta* female.

male age and mating status, and there was no interaction between these two factors (Table 1). The number of follicles increased rapidly after mating and statistically significant differences were recorded between mated and virgin females at the age of three and four days (Table 1). In both virgin and mated females, the ovariole width increased with increase in female age, however, it was significantly wider in mated females than virgin female at ages of 3, 4 and 5 days (Table 1).

Immature eggs were found in the ovarioles of one-two day old mated females, with mature eggs present from day 3 onwards (Table 1; Fig. 3). The number of mature eggs continuously increased with increase in female age regardless of mating status. However, the increase started earlier at three days in mated females, compared to virgin females, which did not have mature eggs until they were five days old (Table 1; Fig. 3). The number of mature eggs differed significantly between virgin and mated females at days 3, 4 and 5. Egg load increased rapidly from four days onwards and was significantly different from that of the virgin females at days 4 and 5 (Table 1).

Table 1. Effect of female age and mating status on ovarian development in *P. dissecta*.

Mating status	Female age (days)	No. of follicles per ovariole	Ovariole width (mm)	Mature eggs	Egg load (number)
Virgin female	1	1.45 ± 0.18$^{a(A)}$	0.20 ± 0.01$^{a(A)}$	No mature eggs present	No mature eggs present
	2	1.50 ± 0.17$^{a(A)}$	0.21 ± 0.03$^{a(A)}$		
	3	2.30 ± 0.26$^{b(A)}$	0.25 ± 0.03$^{a(A)}$		
	4	4.20 ± 0.16$^{c(A)}$	0.28 ± 0.05$^{a(A)}$		
	5	4.20 ± 0.16$^{c(A)}$	0.41 ± 0.03$^{b(A)}$		
Mated female	1	1.50 ± 0.17$^{a(A)}$	0.20 ± 0.01$^{a(A)}$	0.00 ± 0.00^{a}	0.00 ± 0.00^{a}
	2	2.80 ± 0.20$^{b(B)}$	0.21 ± 0.04$^{a(A)}$	0.00 ± 0.00^{a}	0.00 ± 0.00^{a}
	3	4.20 ± 0.16$^{c(B)}$	0.31 ± 0.03$^{b(B)}$	0.60 ± 0.16^{b}	0.20 ± 0.20^{a}
	4	4.20 ± 0.16$^{c(A)}$	0.43 ± 0.02$^{c(B)}$	1.10 ± 0.10^{c}	7.50 ± 0.40^{b}
	5	4.20 ± 0.16$^{c(A)}$	0.62 ± 0.04$^{d(B)}$	1.50 ± 0.17^{d}	8.50 ± 0.34^{c}
$F_{(age)}$		18.16**	52.30**	14.41**	274.41**
$F_{(mating\ status)}$		6.16*	107.76**	149.52**	1469.52**
$F_{(days\ X\ mating\ status)}$		1.75^{NS}	10.52**	9.41**	274.41**

Values are Mean ± SE; * and ** denote F-values significant at $P < 0.01$ and $P < 0.0001$, respectively; NS denotes F-values non-significant at $P > 0.05$. Lower case letters are for comparison of means for female of different ages and upper case letters in parentheses are for comparison of females that have a different mating status.

DISCUSSION

We show for the first time that mating accelerates ovarian development in ladybirds. In addition, this study demonstrates that an increase in age leads to an increase in various ovariole development parameters: the number of follicles, ovariole width, the number of mature eggs and egg load. However, mating significantly hastened this process, so much so that the number of follicles in 3 day old mated females was significantly different from that in similar aged virgin females.

In other insects, the correlation of ovarian development with female age is well established (Rhamhalinghan, 1985; Fortes et al., 2011; Yuan et al., 2013). Egg maturation with age has been attributed to juvenile hormones (JH), sex peptides (SP) and ovulin (Chen et al., 1988; Herndon & Wolfner, 1995; Heifetz et al., 2000, 2005; Chapman et al., 2003; Liu & Kubli, 2003). Juvenile hormones are involved in the synthesis and uptake of vitellogenin in adult female insects (Davey et al., 1993; Glinka & Wyatt, 1996; Tufail et al., 2014), and their levels vary according to the oviposition cycle (Wyatt & Davey, 1996; Borst et al., 2000). Juvenile hormone levels in many insect species are directly correlated with ovarian mass and stage of ovarian development (Koeppe et al., 1985; Okuda & Chinzei, 1988).

In our study, mating accelerated the rate of ovariole development. This is the first time that such an effect has been reported in ladybirds. Such dramatic acceleration may be due to the transfer of seminal fluid proteins and other male chemicals during mating that facilitate ovariole development (Quimio & Walter, 2000; Gillott, 2003). Seminal fluid proteins are known to have a role in influencing yolk allocation, or inactivating genes for faster metabolism in the eggs of multiply mated females (Carvalho et al., 2006). Mating in some insects is also known to be essential for a number of female physiological processes, including, the initiation of vitellogenesis (Jin & Gong, 2001; Uchida et al., 2003), follicle production and maturation, and speed of ovarian development (Brunt, 1971; Horton et al., 2005). Mating is known to stimulate oogenesis in several insect species by triggering a hormonal response, mobilization of reserves, or through providing nutritional material (Gillott & Friedel, 1977; Wheeler, 1996). Although, this is not always so, as in *Nezara viridula* (L.) (Heteroptera: Pentatomidae) and other species of stinkbug, where mating does not influence ovary maturation (Masner, 1966; Davey et al., 1986). In stinkbugs, mating appears to be a key for female oviposition, since virgin females do not lay eggs (Odhiambo & Arora, 1973; Horton et al., 2005).The effects of mating on egg development and oviposition appear, therefore, to be variable within insect orders and even within some genera.

Amongst accessory gland proteins transferred to the females during mating, sex peptides are known to act indirectly on ovariole development via juvenile hormone (Kelly et al., 1987; Ottiger et al., 2000), while ovulin stimulates the release of oocytes from the ovary (Heifetz et al., 2000). In mated females, ovulin perhaps acts directly on the musculature (Heifetz et al., 2000) or through neuroendocrinal targets (Monsma et al., 1990; Lung & Wolfner, 1999). Ovulin is supposed to stimulate the release of mature oocytes (Heifetz et al., 2000; Wolfner, 2002).

Thus, the present study indicates that ovariole development is an age related process, which is accelerated by mating. Mating in ladybirds may stimulate ovariole maturation by the males transferring proteins in their seminal fluid that act either: (i) directly on ovariole development or (ii) indirectly by affecting the genes which regulate vitellogenesis. Further studies are therefore required to help identify the specific factors involved in this process.

ACKNOWLEDGEMENTS. The authors are thankful to S. Paul, Centre for Ecology & Conservation, College of Life & Environmental Sciences, University of Exeter, Penryn, UK for language diting as well as some important suggestions. Department of Higher Education, Govt. of UP, Lucknow is also acknowledged for providing financial assistance under the Center of Excellence programme for this work.

REFERENCES

Adams T.S. 2000: Effect of diet and mating status on ovarian development in a predaceous stink bug *Perillus bioculatus* (Hemiptera: Pentatomidae). — *Ann. Entomol. Soc. Am.* **93**: 529–535.

Andres J.A., Maroja L.S., Bogdanowicz S.M., Swanson W.J. & Harrison R.G. 2006: Molecular evolution of seminal proteins in field crickets. — *Mol. Biol. Evol.* **23**: 1574–1584.

Atlihan R. & Chi H. 2008: Temperature-dependent development and demography of *Scymnus subvillosus* (Coleoptera: Coccinellidae) reared on *Hyalopterus pruni* (Homoptera: Aphididae). — *J. Econ. Entomol.* **101**: 325–333.

Avila F.W., Sirot L.K., Laflamme B.A., Rubinstein C.D. & Wolfner M.F. 2011: Insect seminal fluid proteins: Identification and function. — *Annu. Rev. Entomol.* **56**: 21–40.

Baer B., Heazlewood J.L., Taylor N.L., Eubel H. & Millar A.H. 2009: The seminal fluid proteome of the honeybee *Apis mellifera*. — *Proteomics* **9**: 2085–2097.

Begun D.J., Lindfors H.A., Thompsom M.E. & Holloway A.K. 2006: Recently evolved genes identified from *Drosophila yakuba* and *D. erecta* accessory gland expressed sequence tags. — *Genetics* **172**: 1675–1681.

Blay S. & Yuval B. 1999: Oviposition and fertility in the Mediterranean fruit fly (Diptera: Tephritidae): effect of male and female body size and the availability of sperm. — *Ann. Entomol. Soc. Am.* **92**: 278–284.

Borst D.W., Eskew M.R., Wagner S.J. & Shores K. 2000: Quantification of juvenile hormone III, vitellogenin, and vitellogenin-mRNA during the oviposition cycle of the lubber grasshopper. — *Insect Biochem. Mol. Biol.* **30**: 813–819.

Braswell W.E., Andres J.A., Maroja L.S., Harrison R.G., Howard D.J. & Swanson W.J. 2006: Identification and comparative analysis of accessory gland proteins in Orthoptera. — *Genome* **49**: 1069–1080.

Brent C.S. 2010: Reproduction of the western tarnished plant bug, *Lygus hesperus*, in relation to age, gonadal activity and mating status. — *J. Insect Physiol.* **56**: 28–34.

Brunt A.M. 1971: The histology of the first batch of eggs and their associated tissues in the ovariole of *Dysdercus fasciatus* Signoret (Heteroptera, Pyrrhocoridae) as seen in the light microscope. — *J. Morphol.* **134**: 105–130.

Buning J. 1994: The ovary of Ectognatha. In Büning J. (ed.): *The Insect Ovary: Ultrastructure, Previtellogenic Growth and Evolution.* Chapman & Hall, London, pp. 31–324.

Carvalho G.B., Kapahi P., Anderson D.J. & Benzer S. 2006: Allocrine modulation of feeding behavior by the sex peptide of *Drosophila*. — *Curr. Biol.* **16**: 692–696.

Ceryngier P., Havelka J. & Hodek I. 2004: Mating and activity of gonads in pre-dormant and dormant ladybirds (Coleoptera: Coccinellidae). — *Invert. Reprod. Dev.* **45**: 127–135.

Chapman T., Arnqvist G., Bangham J. & Rowe L. 2003: Sexual conflict. — *Trends Ecol. Evol.* **18**: 41–47.

Chen P.S., Stumm-Zollinger E., Aigaki T., Balmer J., Bienz M. & Bohlen P. 1988: A male accessory gland peptide that regulates reproductive behavior of female *D. melanogaster*. — *Cell* **54**: 291–298.

Choate B.A. & Lundgren J.G. 2013: Why eat extrafloral nectar? Understanding food selection by *Coleomegilla maculata* (Coleoptera: Coccinellidae). — *BioControl* **58**: 359–367.

Davey K.G., Maimetes I.K. & Ruegg R.P. 1986: The relationship between crop size and egg production in *Rhodnius prolixus*. — *Can. J. Zool.* **64**: 2654–2657.

Davey K.G., Sevala V.S. & Gordan D.R.B. 1993: The action of juvenile hormone and antigonadotropin on the follicle cells of *Locusta migratoria*. — *Invertebr. Reprod. Devel.* **24**: 39–45.

Ferrer A., Dixon A.F.G. & Hemptinne J.L. 2008: Prey preference of ladybird larvae and its impact on larval mortality, some life-history traits of adults and female fitness. — *Bull. Insectol.* **61**: 5–10.

Findlay G.D., Yi X., Maccoss M.J. & Swanson W.J. 2008: Proteomics reveals novel *Drosophila* seminal fluid proteins transferred at mating. — *PLoS Biol.* **6**: 178.

Fortes P., Salavador G. & Consoli F.L. 2011: Systematics, morphology and physiology, ovary development and maturation on in *Nezara viridula* (L.) (Hemiptera: Pentatomidae). — *Neotrop. Entomol.* **40**: 89–96.

Gillott C. 2003: Male accessory gland secretions: modulators of female reproductive physiology and behavior. — *Annu. Rev. Entomol*. **48**: 163–184.

Gillott C. & Friedel T. 1977: Fecundity enhancing and receptivity-inhibiting substances produced by male insects: a review. — *Adv. Invertebr. Reprod.* **1**: 199–218.

Glinka A.V. & Wyatt G.R. 1996: Juvenile hormone activation of gene transcription in locust fat body. — *Insect Biochem. Mol. Biol.* **26**: 13–18.

Heifetz Y., Lung O., Frongillo E.A. Jr & Wolfner M.F. 2000: The *Drosophila* seminal fluid protein Acp26Aa stimulates release of oocytes by the ovary. — *Curr. Biol.* **10**: 99–102.

Heifetz Y., Vandenberg L.N., Cohn H.I. & Wolfner M.F. 2005: Two cleavage products of the *Drosophila* accessory gland protein ovulin can independently induce ovulation. — *Proc. Natl. Acad. Sci. U.S.A.* **102**: 743–748.

Heming B.S. 2003: *Insect Development and Evolution.* Cornell University Press, Ithaca, NY, 444 pp.

Herndon L.A. & Wolfner M.F. 1995: A *Drosophila* seminal fluid protein, Acp26Aa, stimulates egg laying in females for 1 day after mating. — *Proc. Natl. Acad. Sci. U.S.A.* **92**: 10114–10118.

Hodek I. & Ceryngier P. 2000: Sexual activity in Coccinellidae (Coleoptera); a review. — *Eur. J. Entomol*. **97**: 449–456.

Hodek I. 2011: Diapause / Dormancy. In Hodek I., Van Emden H.F. & Honek A. (eds): *Ecology and Behaviour of the Ladybird (Coccinellidae).* John Wiley and Sons, Oxford, pp. 275–342.

Hodek I., Van Emden H.F. & Honek A. 2011: *Ecology and Behaviour of the Ladybird (Coccinellidae).* John Wiley and Sons, Oxford, 578 pp.

Horton D.H., Lewis T.M. & Neven L.G. 2005: Ovarian development and lipid reserves are affected by mating delays in three species of *Anthocoris* (Hemiptera: Anthocoridae). — *Can. Entomol.* **137**: 328–336.

Jarvis M.A. & Copland M.J.W. 1996: The life cycle. In Jarvis M. & Kidd N. (eds): *Insect Natural Enemies, Practical Approaches to their Study and Evolution*. Chapman and Hall, New York, pp. 63–161.

Jin Z.Y. & Gong H. 2001: Male accessory gland derived factors stimulate oogenesis and enhance oviposition in *Helicoverpa armigera* (Lepidoptera: Noctuidae). — *Arch. Insect Biochem. Physiol.* **46**: 175–185.

Kawazu K., Ichiki R.T., Dang D.T. & Nakamura S. 2011: Mating sequence and evidence for the existence of female contact sex pheromone in *Brontispa longissima* (Coleoptera: Chrysomelidae). — *Jpn. Agric. Res. Quart.* **45**: 99–106.

Kawazu K., Sugeno W., Mochizuki A., Shun-Ichiro Takano S.I., Murata M., Ichiki R.T. & Nakamuara S. 2012: Age in relation to copulation, egg development, and multiple mating behavior in the coconut palm pest *Brontispa longissima* (Coleoptera: Chrysomelidae). — *Ann. Entomol. Soc. Am.* **105**: 746–750.

Kelly T.J., Adams T.S., Schwartz M.B., Birnbaum M.J., Rubenstein E.C. & Imberski R.B. 1987: Juvenile hormone and ovarian maturation in the Diptera: A review of recent results. — *Insect Biochem.* **17**: 1089–1093.

Koeppe J.K., Fuchs M., Chen T.T., Hunt L.M., Kovalick G.E. & Briers T. 1985: The role of juvenile hormone in reproduction. In Kerkut G.A. & Gilbert L.I. (eds): *Comprehensive Insect Physiology, Biochemistry and Pharmacology. Vol. 8.* Pergamon, Oxford, pp. 165–205.

Liu H. & Kubli E. 2003: Sex-peptide is the molecular basis of the sperm effect in *Drosophila melanogaster*. — *Proc. Natl. Acad. Sci. U.S.A.* **100**: 9929–9933.

Lung O. & Wolfner M.F. 1999: *Drosophila* seminal fluid proteins enter the circulatory system of the mated female fly by crossing the posterior vaginal wall. — *Insect Biochem. Mol. Biol.* **29**: 1043–1052.

Masner P. 1966: The structure, function and imaginal development of the female inner reproductive organs of *Adelphocoris lineolatus* (Goeze) (Heteroptera: Miridae). — *Acta Entomol. Bohemslov.* **63**: 177–199.

Monsma S.A., Harada H.A. & Wolfner M.F. 1990: Synthesis of two *Drosophila* male accessory gland proteins and their fate after transfer to the female during mating. — *Dev. Biol.* **142**: 465–475.

Mueller J.L., Ravi Ram K., McGraw L.A., Bloch Qazi M.C., Siggia E.D., Clark A.G., Aquadro C.F. & Wolfner M.F. 2005: Cross-species comparison of *Drosophila* male accessory gland protein genes. — *Genetics* **171**: 131–143.

Nedved O. & Honek A. 2011: Life history and development. In Hodek I., Van Emden H.F. & Honek A. (eds): *Ecology and Behaviour of the Ladybird (Coccinellidae)*. John Wiley and Sons, Oxford, pp. 54–109.

Odhiambo T.R. & Arora G.K. 1973: A comparative study of oocyte development in cotton stainers (*Dysdercus* spp., Pyrrhocoridae) and the factors that control egg production. — *Entomol. Exp. Appl.* **16**: 455–470.

Okuda T. & Chinzei Y. 1988: Vitellogenesis in a lady-beetle, *Coccinella septempunctata* in relation to the aestivation diapause. — *J. Insect Physiol.* **34**: 393–401.

Omkar & Pervez A. 2000: Sexual dimorphism in *Propylea dissecta* (Mulsant), (Coccinellidae: Coleoptera). — *J. Aphidol.* **14**: 139–140.

Omkar & Mishra G. 2005: Preference-performance of a generalist predatory ladybird: A laboratory study. — *Biol. Contr.* **34**: 187–195.

Omkar & Pervez A. 2005: Mating behaviour of an aphidophagous ladybird beetle, *Propylea dissecta* (Mulsant). — *Insect Sci.* **12**: 37–44.

Osawa N. 2005: The effect of prey availability on ovarian development and oosorption in the ladybird beetle *Harmonia axyridis* (Coleoptera: Coccinellidae). — *Eur. J. Entomol.* **102**: 503–511.

Ottiger M., Soller M., Stocker R.F. & Kubli E. 2000: Binding sites of *Drosophila melanogaster* sex peptide pheromones. — *J. Neurobiol.* **44**: 57–71.

Papaj D.R. 2000: Ovarian dynamics and host use. — *Annu. Rev. Entomol.* **45**: 423–448.

Quimio G.M. & Walter G.H. 2000: Swarming, delayed sexual maturation of males, and mating behavior of *Fopius arisanus* (Sonan) (Hymenoptera: Braconidae). — *J. Insect Behav.* **13**: 797–813.

Rhamhalinghan M. 1985: Intraspecific variations in ovariole number/ovary in *Coccinella septempunctata* L. (Coleoptera: Coccinellidae). — *Indian Zool.* **9**: 91–97.

Ryall K.L., Dutkiewicz D., Silk P.J., Antunes P.M. & Ochoa I. 2013: Ovarian development of *Agrilus planipennis*: effects of age and mating status and influence on attraction to host volatiles. — *Entomol. Exp. Appl.* **149**: 77–84.

Simmons L.W. 2011: Inbreeding depression in the competitive fertilization success of male crickets. — *J. Evol. Biol.* **24**: 415–421.

Tufail M., Nagaba Y., Elgendy A.M. & Takeda M. 2014: Regulation of vitellogenin genes in insects. — *Entomol. Sci*. **17**: 269–282.

Uchida K., Moribayashi A., Matsuoka H. & Oda T. 2003: Effects of mating on oogenesis induced by amino acid infusion, amino acid feeding, or blood feeding in the mosquito *Anopheles stephensi* (Diptera: Culicidae). — *J. Med. Entomol.* **40**: 441–446.

Uzsak A. & Schal C. 2012: Differential physiological responses of the German cockroach to social interactions during the ovarian cycle. — *J. Exp. Biol.* **215**: 3037–3044.

Uzsak A. & Schal C. 2013: Sensory cues involved in social facilitation of reproduction in *Blattella germanica* females. — *PLoS One* **8**(2): e55678, 10 pp.

Wagstaff B.J. & Begun D.J. 2005: Comparative genomics of accessory gland protein genes in *Drosophila melanogaster* and *D. pseudoobscura*. — *Mol. Biol. Evol.* **22**: 818–832.

Walker M.J., Rylett C.M., Keen J.N., Audsley N., Sajid M., Shirras A.D. & Isaac R.E. 2006: Proteomic identification of *Drosophila melanogaster* male accessory gland proteins, including a pro-cathepsin and a soluble gamma-glutamyltranspeptidase. — *Proteome Sci.* **4**:9, 10 pp.

Walters J.R. & Harrison R.G. 2008: EST analysis of male accessory glands from *Heliconius* butterflies with divergent mating systems. — *BMC Genomics* **9**:592, 13 pp.

Walters J.R. & Harrison R.G. 2010: Combined EST and proteomic analysis identifies rapidly evolving seminal fluid proteins in *Heliconius* butterflies. — *Mol. Biol. Evol.* **27**: 2000–2013.

Wang S., Tan X.L., Guo X.J. & Zhang F. 2013: Effect of temperature and photoperiod on the development, reproduction, and predation of the predatory ladybird *Cheilomenes sexmaculata* (Coleoptera: Coccinellidae). — *J. Econ. Entomol.* **106**: 2621–2629.

Ware R.L., Ramon-Portugal F., Magro A., Ducamp C., Hemptine J.L. & Majerus M.E.N. 2008: Chemical protection of *Calvia quatuordecimguttata* eggs against intraguild predation by the invasive ladybird *Harmonia axyridis*. — *BioControl* **53**: 189–200.

Wheeler D. 1996: The role of nourishment in oogenesis. — *Annu. Rev. Entomol.* **41**: 407–431.

Wolfner M.F. 2002: The gifts that keep on giving: physiological functions and evolutionary dynamics of male seminal proteins in *Drosophila*. — *Heredity* **88**: 85–93.

Wyatt G.R. & Davey K.G. 1996: Cellular and molecular actions of juvenile hormone. 2. Roles of juvenile hormone in adult insects. — *Adv. J. Insect Physiol.* **26**: 1–155.

Yamane T., Goenaga J., Ronn J.L. & Arnqvist G. 2015: Male seminal fluid substances affect sperm competition success and female reproductive behavior in a seed beetle. — *PLoS One* **10**(4): e0123770, 14 pp.

Yuan W., Li W., Li Y. & Wu K.G. 2013: Combination of plant and insect eggs as food sources facilitates ovarian development in an omnivorous bug *Apolygus lucorum* (Hemiptera: Miridae). — *J. Econ. Entomol.* **106**: 1200–1208.

Received May 18, 2015; revised and accepted September 14, 2015
Published online January 8, 2016