Journal of Animal & Plant Sciences, 35(1): 2025, Page: 186-196
ISSN (print): 1018-7081; ISSN (online): 2309-8694
https://doi.org/10.36899/JAPS.2025.1.0014

IMPACT OF MATERNAL REARING DENSITY ON LIFE HISTORY TRAITS OF *MYTHIMNA SEPARATA* (WALKER)

A. W. Solangi[1], Y. Cheng[2], L. Zhang[2] and X. Jiang[2, *],

[1]Department of Plant Protection, Faculty of Crop Protection, Sindh Agriculture University, Tandojam-Pakistan.
[2]State Key Laboratory for Biology of Plant Diseases and Insect Pests, Institute of Plant Protection, Chinese Academy of Agricultural Sciences, Beijing, China.
*Corresponding author's Email: xfjiang@ippcaas.cn

ABSTRACT

Migratory insects employ various adaptive strategies during alterations in the maternal environment, such as maternal rearing (Isolation, moderate, or crowding) which significantly affect their offspring's survival, development, reproduction, and onset of migration. While previous studies have mainly concentrated on the impact of varying temperature conditions on insect populations, the effects of changes in maternal rearing density on their progeny have been given relatively less attention. The current study emphasizes the impact of maternal rearing density on the offspring's life history traits in the *Mythimna separata*. Eggs were collected from laboratory stock and newly hatched larvae from maternal design split into three density regimes and reared at densities of low-density (L_D) 1 larva, moderate density (M_D) 10 larva, and high density (H_D) 20 Larva per 800-ml jar with the diameter of 10cm. For initiation of the next generation, 400 females were selected from the maternal design and kept per combination for offspring larval density, eggs laid by mothers were collected and offspring were again divided into three groups and exposed to (L_D), (M_D), and (H_D). Results demonstrated that the development time of offspring was shortened (31.62±1.14 days) after maternal high-density rearing with a significant difference, offspring's pupal mass significantly decreased (211±7.58 mg) at stressed conditions. Low-density reared mothers laid fewer eggs (480±28.63) as compared to crowded mothers (718±45.52) eggs with significant differences. Offsprings whose mothers were raised at moderate density displayed the greatest, and offspring raised in isolation had the poorest flight capability relative to high density. Maternal larval density had a significant impact on the offspring pre-oviposition period (POP), offspring with longer POP usually showed more significant flight potential, also POP of all offspring density regimes had an essential and positive correlation with total flight distance, L_D ($P=0.001$; $R^2=0.99$), M_D ($P=0.002$; $R^2=0.99$) and H_D offspring's ($P=0.001$; $R^2=0.98$). However, moderate and high-density offspring negatively correlated with total flight duration (R^2-0.43) and (R^2-0.48), respectively. In conclusion, the maternal rearing environment imposes phenotypic changes on offspring life history traits, and flight-induced changes in maternal egg provisioning had direct consequences for offspring growth and survival across each life stage from egg to adulthood.

Keywords: Maternal effect, density, offspring development, reproductive plasticity, flight performance.

INTRODUCTION

Oriental armyworm, *Mythimna separata* (Walker) (Lepidoptera: Noctuidae), is a severe migratory insect pest and responsible for 20-60% of economic losses in grain crops (Solangi *et al*., 2021; Lv *et al*., 2022; Xu *et al*., 2023). The environmental conditions (Temperature, photoperiod, and nutrients) experienced by the parents may impact the life history traits of the next generation (Solangi *et al*., 2021; Ding *et al*., 2024) and are referred to as the maternal effect (Rossiter, 1996; Bernardo, 1996; Benton *et al*., 2008; Palacios *et al*., 2022). These effects are frequently observed as evolutionary optimization processes that increase the adaptation of offspring to future environments (Rotem *et al*., 2003). Maternal effects can also be understood as reactions to limitations imposed by the mother's physiological state (Moore and Harris, 2003). Adaptive maternal effects occur when a mother's response to environmental cues enhances her offsprings fitness, increasing their chances of survival and reproduction (Mousseau and Fox, 1998). The impact of the mother's exposure to population density on the characteristics of her offspring illustrates the challenge of distinguishing between adaptive interpretations and those that involve limitations (Zuk and Stoehr, 2002). From an adaptive viewpoint, high population density might signal a potential for future competition among offsprings for resources like food, mates, or oviposition sites (Pexton and Mayhew, 2005; Allen *et al*., 2008). Alternatively, elevated larval crowding might impact female reproduction, leading to a potential decrease in the production of fewer offspring, smaller size, and inferior quality (Jervis *et al*., 2005). These circumstances could also result in increased mortality rates among these females when contrasted with mothers raised under conditions of lower population density (Arbab, 2014). Instances illustrating unfavorable and non-beneficial outcomes of adult crowding encompass cases such as the diminished lifespan and fertility observed in *Chilo partellus* (Dhillon *et al*., 2018) and a reduction in reproductive capacity. Nevertheless, there has been a growing focus on maternal effects rooted in nutrition (Atkinson *et al*., 2001), where changes in the quantity or quality of nutritional resources in eggs occur due to factors related to population density that predominantly impact moths during their larval stage (Rossiter, 1991). While this phenomenon has only been recorded in a limited number of insect species, i.e., *Lymantria dispar* (L.) the concept of nutritionally based maternal effects has been suggested as a potential explanation for delayed responses and cyclic shifts in population density following declines in outbreaks (Rossiter, 1996; Steigenga *et al*., 2005). Adult insects that experience crowding and food stress during early life tend to move away from deteriorating habitats (Khuhro *et al*., 2014). The aim of the current study is to investigate the significance of habitat and physiological factors that exert non-genetic fitness effects, which could help us to monitor and forecast accurately the occurrence of *M. separata*. This could have important consequences for the population dynamics of this noxious insect pest.

MATERIALS AND METHODS

Breeding design: The eggs were collected from a large, outbred laboratory population of *M. separata* from the Institute of Plant Protection, Chinese Academy of Agricultural Sciences (CAAS), Beijing, China, with 300-400 individuals per generation. In an insect-rearing chamber, newly hatched larvae (10-20 larvae/800 mL jar) were reared under favorable environmental conditions (temperature: 24-1°C; relative humidity: 70±5%) and photoperiod: L14: D10). Fresh maize leaves were provided daily until pupal formation and adult emergence. The virgin pair was left undistributed for mating, after mating 400 females were selected randomly from this laboratory stock and placed separately in netted cages (1 m^3) with a 2-ml vial containing 5% honey solution (Luo, 1995; Jiang *et al*., 2000; Solangi *et al*., 2021).

Maternal larval density design: These females (n=400) will subsequently be referred to as the maternal treatment; after mating on the first day of oviposition, eggs were collected and counted from all boxes, and newly hatched larvae split into three density regimes and reared at densities of low-density (L_D) 1 larva/jar, moderate density (M_D) 10 larvae/jar and high density (H_D) 20 larvae/jar lines per 800-ml jar with the diameter of 10cm. Fresh leaves of maize seedlings were provided every day throughout the feeding period of the larva. The rearing design for one exemplary replicate is shown in Fig. 1.

Offspring generation breading design: For measurements of life history traits of offspring, 400 females were selected from the maternal design and kept per combination for offspring larval density. To initiate the next generation, eggs laid by mothers were collected and offsprings were again divided into three groups and exposed to (L_D), (M_D), and (H_D). The following procedures were adopted to assess the life-history traits of offspring.

Development time estimation: The offspring's development time (days) in all larval stages from the first egg deposit by the adult was counted individually up to the pupal stage (Solangi *et al*., 2021).

Pupal weight assessment: The three-day-old pupae were weighed on an electronic balance (Shimadzu, China) and placed in 50-cm^4 cages (Solangi *et al*., 2021).

Assessment of flight parameters: For measuring flight parameters, one-day-old moths (n=40) were derived from each larval density regime and determined by a computer-aided flight mill system, as described in our previous studies (Jiang *et al*., 2000; Solangi *et al*., 2021). The moths were slightly sedated in a glass tube (2-8 cm) with an ether-soaked cotton wick to aid in the attachment of tethers. The copper wire used for the tether had a diameter of 0.25 mm, with a 1-mm loop at one end and a 2-cm straight section running vertically to the loop. After brushing away the scales and hairs at the attachment location, the loop was glued to the dorsal surface of the junction between the metathorax and the abdomen using super glue. Before being attached to the flying mill's arm, the tethered moth was kept in a 50ml vial. A modified 32-channel flight mill system was used for the flying tests. The flight performance tests were conducted in a dark climatic room; the flying room's temperature and humidity were kept at 24-1°C and 70-10% R.H, respectively, to support *M. separata's* maximal flight capability. The data recording session started at 19:00 and ended at 07:00 the next day, the actual time of *M. separata* migration in the field (Feng *et al*., 2004). The analysis did not include whether the moth broke a wing during the test time or separated from the tether. The flight performance of the moths was assessed by utilizing the standards of Zhang *et al*. (2020).

Pre-oviposition period (Days): Newly 100 emerged female and male pairs were sexed and placed into 2-L plastic boxes with a 2-mL vial containing a 15% honey (wt: vol) solution. The time between the moths' appearance and the first egg laid is known as the pre-oviposition phase. Food was replaced, and cages were regularly inspected for the presence of eggs.

Fecundity: Total female fecundity was determined by counting the number of eggs produced each day until the female death, as previously observed by Jiang *et al.* (2000).

Adult longevity (Days): Adult longevity was observed from the day the adult emerged from pupae until mortality; it is generally called the total life span of the adult.

Statistical analyses: Statistical analyses were carried out to examine the difference between density regimes, followed by a Tukey's HSD (honestly significant difference) by using a two-way analysis of variance (ANOVA) through SPSS advanced software (IBM 21 version), significant differences were investigated at least significant differences (LSD) by applying post hoc tests. The relationship between the oviposition period and flight potential for all treatments was evaluated through XLSTAT version 2018 and Originpro 2015.

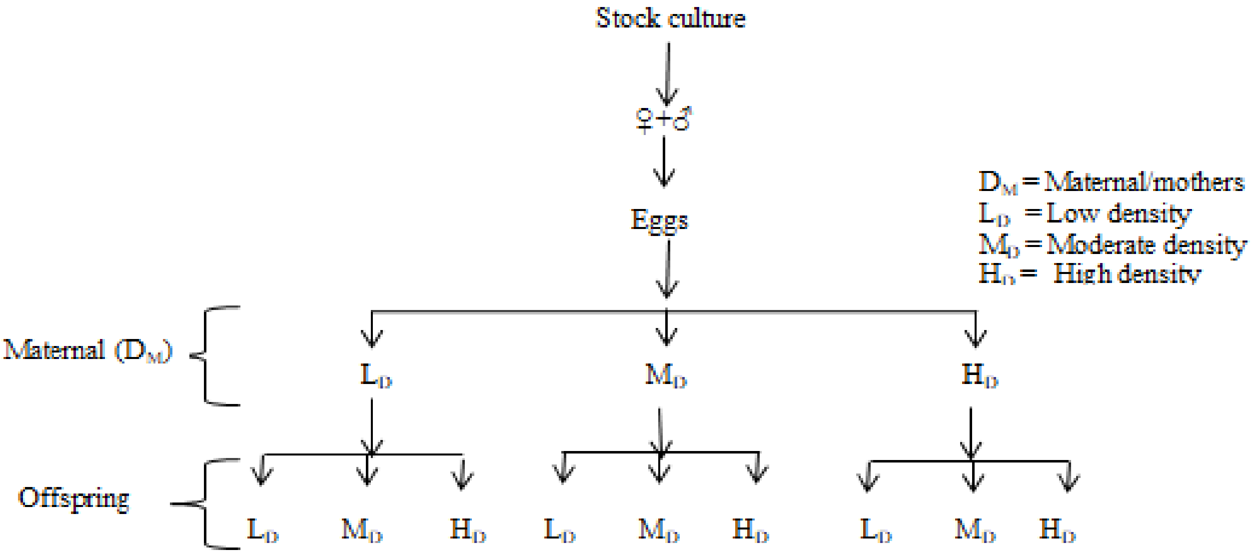

Figure 1. Rearing design, exemplified for one of the 400 replicate families, with D_M = Maternal density (density at which the parents were reared), L_D=Low density (1 larvae/jar), M_D=Moderate density (10 larvae/jar) and H_D =High density (20 larvae/jar).

RESULTS

In the *M. separata*, larval density regimes experienced by the mothers had significant effects on the expression of three of four considered life-history traits of their offspring.

Development time (Days): Developmental time (days) was significantly affected by maternal density (D_M). The effect of maternal density on developmental time varied depending on maternal larval density/jar. It was observed that development time was longer (43.86±2.36) when parent larvae were raised at one larvae/jar in all respective offspring lines with significant differences. Offsprings whose parents were reared at moderate and high density had shorter development periods (38.62±1.14 days). However, there were significant differences between all offspring density regimes (Fig. 2C; Table 1).

Pupal weight (mg): Maternal larval density significantly affected the fresh weight of pupae; pupae were heavier (344.15±22.63 mg) when mothers were reared at the low-density line. The lowest (227.05±16.36 mg) pupal mass was observed whose mothers were reared at moderate and high density. There was a significant difference between offspring and mothers' density regimes (Fig. 2 B; Table 1).

Pre-oviposition period (Days): Females from the moderate density had significantly more extended pre-oviposition period than the other density regimes. However, it differed in each offspring line (L_D: 5±0.10 days; M_D: 6±0.22 days; H_D: 5.3 ±0.15days) (Fig. 2C; Table 1).

Table 1 Results of (ANOVA) analysis for the effects of maternal larval density (D_M) on offspring development time, pupal weight, and preoviposition period.

Density regimes	Development time				Pupal weight				Pre oviposition period			
	DF	Error	MS	P	DF	Error	MS	P	DF	Error	MS	P
D_M Maternal	2	72	253.36	0.001	2	297	4452.12	0.001	2	72	2587.91	0.001
L_D *offspring*	2	72	8936.01	0.001	2	144	1059.3	0.005	2	72	4026.30	0.001
M_D *offspring*	2	72	4789.15	0.023	2	144	228.26	0.001	2	72	2069.2	0.001
H_D *offspring*	2	72	784.88	0.005	2	144	478.10	0.018	2	72	478.20	0.001

DF=Degree of freedom, MS= Mean square, P=Probability

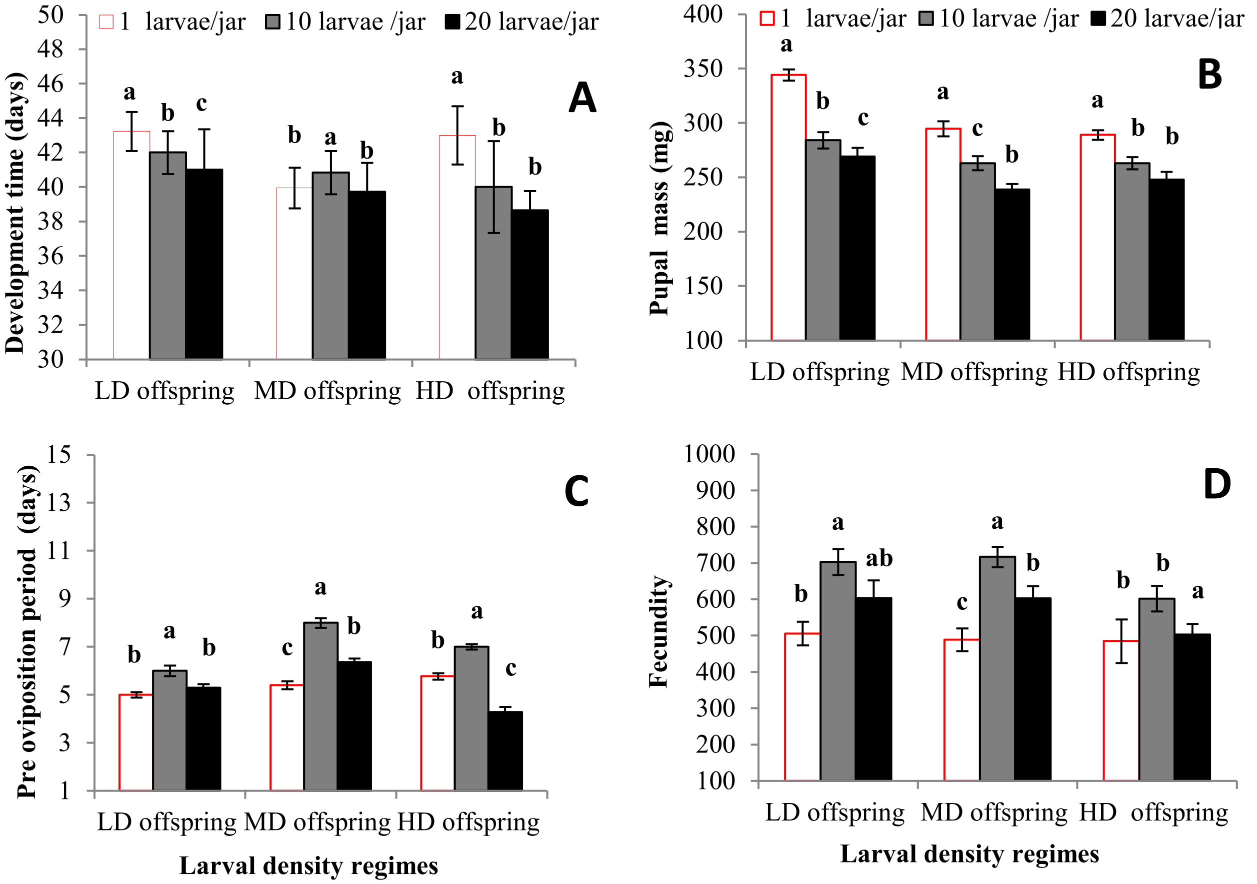

Figure 2. Impact of maternal larval rearing density on offspring development period (A), pupal weight (B), pre-oviposition period (C), and female fecundity (D). The different alphabetical letters indicate the significant differences between density lines. L_D=Low density (1 larvae/jar), M_D = Moderate density (10 larvae/jar) and H_D =High density (20 larvae/jar).

Fecundity: Lifetime egg production was significantly affected by maternal larval density; moderate-density reared mothers laid more (708.0±37.0) eggs as compared to low and high-density reared, and there was not a significant difference between low-density offspring's regimes, most substantial and consistent egg production was observed in moderate density offsprings regimes with significant differences than at high-density offsprings regimes (Fig. 2D; Table 2).

Female and male longevity (Days): Offsprings whose mothers were reared at low density had a shorter (9.1±0.83 days) lifespan and insignificant differences between low-density offspring regimes. Overall, moderate-density and high-density offspring spent a long-life span (13.0±1.25 days) and (11.19 ±1.02 days) respectively, significant differences were observed among treatments (Fig.3 A). Similar trends were observed in the male life span, shorter lifespan (L_D: 8.96.93±0.20; M_D: 12.72±0.28; H_D: 11.90±0.36 days) were observed as compared to other density regimes. There were significant differences between low and moderate-density offspring, but no significant differences were recorded between high-density offspring regimes (Fig. 3 B; Table 2).

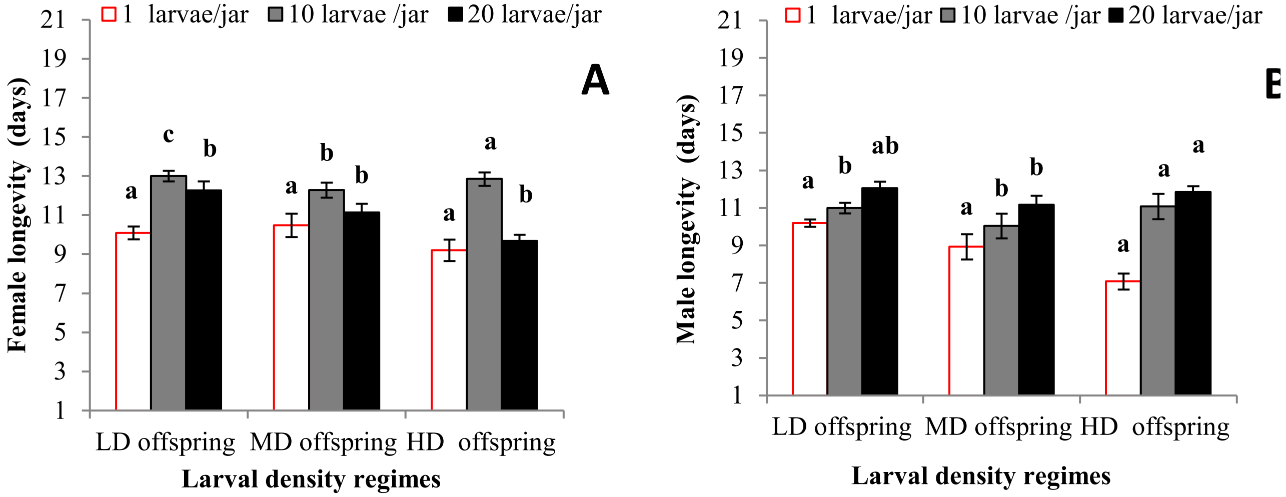

Figure 3. Impact of maternal larval rearing density on offspring longevity, (A) female and (B) male longevity (Days). The different alphabetical letters indicate the significant differences between density regimes. L_D=Low density (1 larvae/jar), M_D = Moderate density (10 larvae/jar) and H_D =High density (20 larvae/jar).

Table 2. Results of (ANOVA) analysis for the effects of maternal larval density (D_M) on offspring fecundity, female and male longevity (Days).

Density regimes	Fecundity				Female longevity				Male longevity			
	DF	Error	MS	P	DF	Error	MS	P	DF	Error	MS	P
D_M Maternal	2	72	872.4	0.001	2	72	7103.2	0.083	2	72	769.2	0.001
L_D *offspring*	2	72	7589.21	0.003	2	72	256.1	0.001	2	72	6656.4	0.037
M_D *offspring*	2	72	23452.02	0.007	2	72	223.02	0.001	2	72	641.90	0.023
H_D *offspring*	2	72	7415.23	0.025	2	72	189.27	0.001	2	72	331.50	0.256

DF=Degree of freedom, MS= Mean square, P=Probability

Flight potential: Maternal larval density significantly affected the flight potential, duration, distance, velocity, and longest flight duration. Offspring whose mothers were raised at moderate density showed the highest (253.53±13.56 minutes) flight duration as compared to isolation rearing generation and had the poorest (180.53 ± 12.45 minutes) flight duration relative to high density, but there was a non-significant difference between the moderate density line which is the remarkable evidence of maternal rearing conditions. Similarly, offspring moths from the moderate density line covered more flight distance as compared to the isolated and crowded density line, the low-density offspring line ($L_{D:}$ 8.43 ± 0.6 km; $M_{D:}$ 17.04 ± 1.18 km and $H_{D:}$ 12.68 ± 0.83 km). Mean flight speed of low-density regimes; ($L_{D:}$ 2.83 ± 0.08 km/h; $M_{D:}$ 5.3 ± 0.14 km/h and $H_{D:}$ 4.71 ± 0.12 km/h), moderate density line ($L_{D:}$ 3.88 ± 0.15 km/h, $M_{D:}$ 4.62 ± 0.14km/h and $H_{D:}$ 4.09 ± 0.13 km/h) and high-density line ($L_{D:}$2.83 ± 0.16km/h; $M_{D:}$ 4.83 ± 0.09 km/h and $H_{D:}$4.22 ± 0.11km/h) with significant difference (Table 3). The longest flight duration of the low-density line was (L_D: 276.0±12.23; M_D: 372.0±15.04 and H_D: 312.0±14.35 minutes) which was a significantly longer flight than isolated and crowded maternal conditions (Fig. 4; Table 3).

Relationship between pre-oviposition period flight parameters: Moderate-density offspring had the most extended pre-oviposition period, with significant differences in low-density and high-density offspring had the shortest pre-oviposition period. The oviposition period of all offspring density regimes had a significant and positive correlation with total flight distance, low

(P=0.001; R^2=0.99; Fig. 5 A), moderate (P=0.002; R^2=0.99; fig. 5 B) and high-density offspring's (P=0.032; R^2=0.98; Fig. 5 C) respectively. Low-density offspring significantly and positively correlated with total flight duration (P=0.001; R^2=0.97; fig. 5 D). However, moderate and high-density offspring negatively correlated with total flight duration only (P=0.001; R^2-0.43 Fig. 5 E: R^2-0.48; Fig. 5 F).

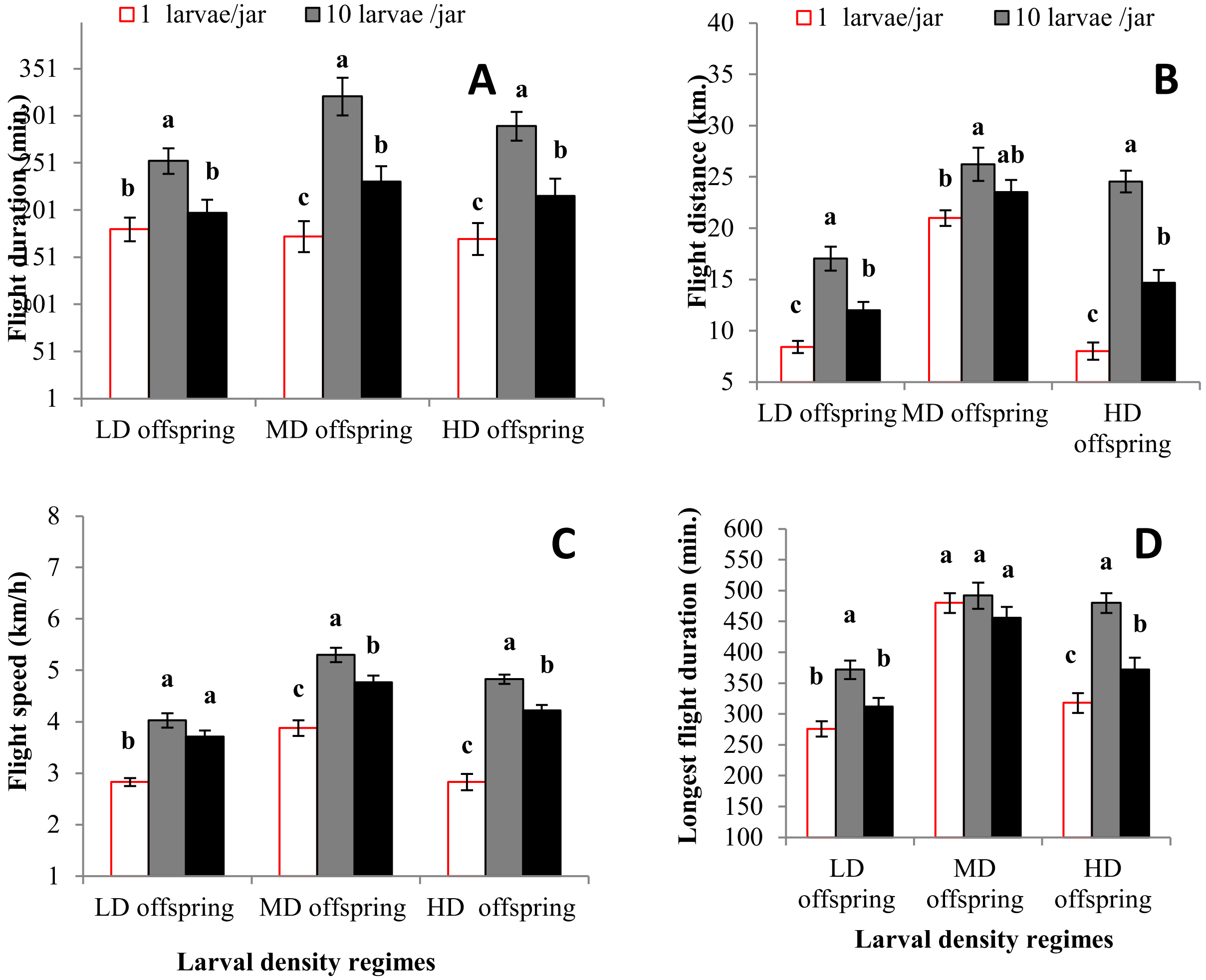

Figure 4. Impact of maternal larval rearing density on offspring flight parameters, flight duration (A), flight distance B), flight speed (C), and longest flight duration (D). The different alphabetical letters indicate the significant differences between density regimes. L_D=Low density (1 larvae/jar), M_D = Moderate density (10 larvae/jar) and H_D =High density (20 larvae/jar).

Table 3. Results of (ANOVA) analysis for the effects of maternal larval density (D_M) on offspring flight duration, distance, and flight velocity in *M. separata*.

Density regimes	Total flight duration				Total flight distance				Flight velocity			
	DF	Error	MS	P	DF	Error	MS	P	DF	Error	MS	P
D_M Maternal	2	99	556.01	0.001	2	99	661.2	0.001	2	99	8726.6	0.001
L_D *offspring*	2	82	1146.6	0.001	2	82	7025.01	0.001	2	82	4156.21	0.003
M_D *offspring*	2	82	790.46	0.001	2	82	213.87	0.032	2	82	912.63	0.001
H_D *offspring*	2	83	449.03	0.001	2	83	1036.3	0.001	2	83	2289.3	0.001

DF=Degree of freedom, MS= Mean square, P=Probability

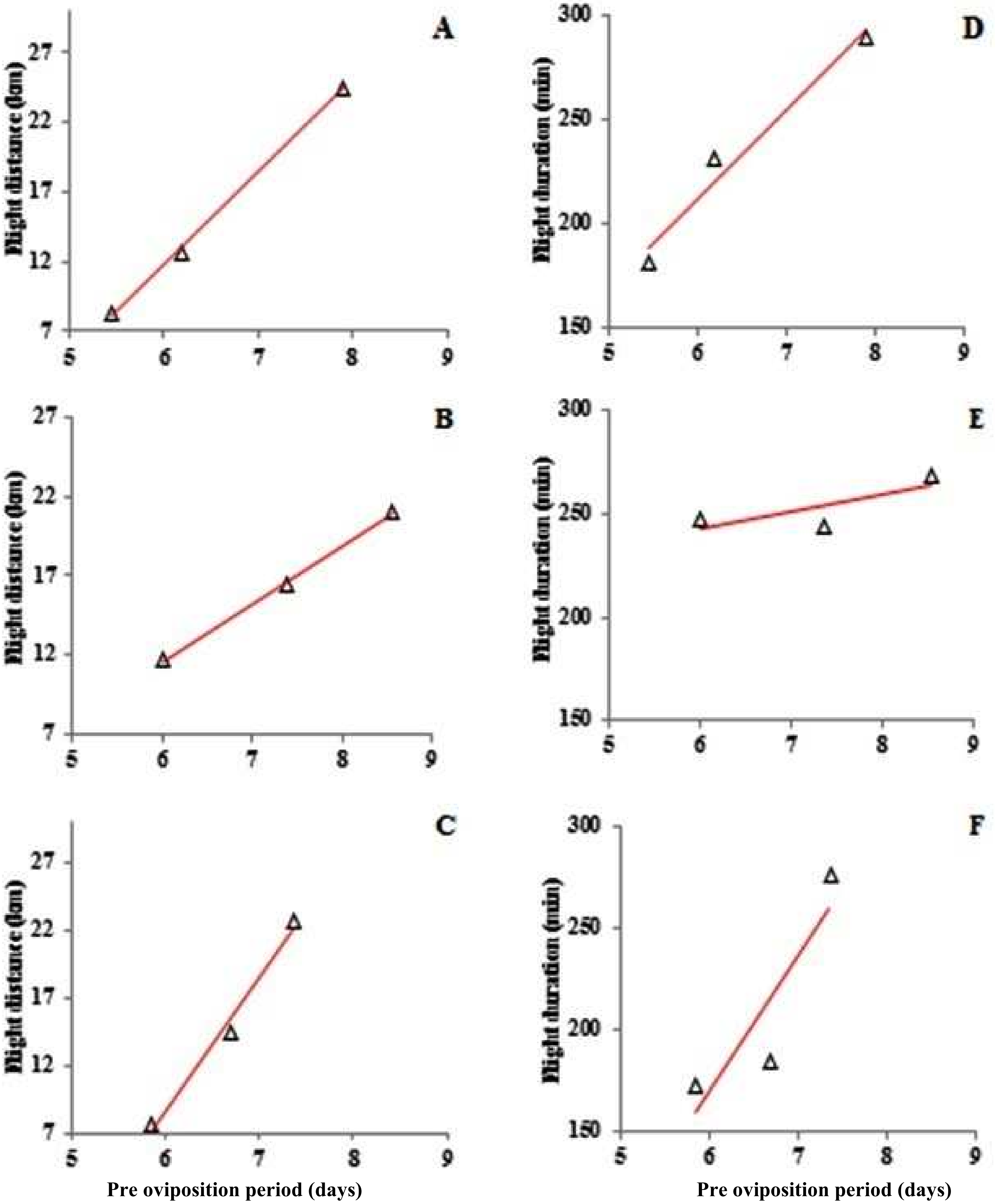

Figure 5. Linear relationship between flight parameters & pre-oviposition period (Days), total flight distance (A: y= 6.64x-28.00 r =0.99, B; y3.36 x – 10.17 r =0.99, C: 9.86 x-50.46 r= 0.98,) or total flight duration (D: y= 42.80x-44.34 r= 0.96, E: y =8.14 x +194.01 r =-0.43, F y=65.99 x-225.93 r= -0.48). Flight distance, A: L_D=Low density (1 larvae/jar), B: M_D = Moderate density (10 larvae/jar), C: H_D =High density (20 larvae/jar). Flight duration, D: L_D=Low density, E: M_D = Moderate density, F: H_D =High density.

DISCUSSION

Migratory insects employ various adaptive strategies during alterations in the maternal environment, such as maternal rearing (Isolation, moderate, or crowding) which significantly affect their offspring's survival, development, reproduction, and onset of migration. Significant variations were observed between larvae from stressed and unstressed populations during current successive research periods at the individual, family, and population levels. Maternal density affects (either direct or indirect) the reproductive plasticity of insects (Myers and Cory, 2013). In pine looper, *Bupalus piniaria*, a decline in pupal weight and reproductive output has been previously observed with different density variations by Kendall *et al.* (2005), similar effects were observed during the current study, the pupal mass also affected egg-to-adult survival of the offspring generation indicating the presence of maternal effects. In Lepidopterous insects, competition within the same species during the early stages of development can negatively impact adult behavior and various life-history traits (Sanghvi *et al.*, 2021). Additionally, overcrowding during growth can lead to alterations in the size and proportion of different morphological traits, causing shifts in allometry (Boggs and Niitepold, 2016). Results of the current study agree with previous studies which support the current hypothesis "maternal density affects the life history traits of offspring" as previously documented on *Stator prunings* (Fox and Czesak, 2000) *Pararge aegeria* (Gibs *et al.*, 2010), gypsy moth (Mark *et al.*, 2000) and *Copidosoma koehleri* (Morag *et al.*, 2011). Moderate-density mothers produce faster-developing, strong fliers, with longest pre-oviposition period offsprings as compared with offsprings of low-density mothers as previously documented such as the rice leaf folder, *Cnaphalocrosis medinalis* Guenee (Yang *et al.*, 2015), beet webworm, *Loxostege sticticalis* L. (Kong *et al.*, 2013), and the African armyworm, *Spodoptera exempta* Walker (Wang *et al.*, 2008). In agreement with previous studies conducted by Morag *et al.* (2011) high maternal density had short development periods, which is evidence of maternal resource transmission, these results agreement agree with Morag *et al.* (2011) who studied the impact of maternal rearing density on next generation of gypsy moths. Maternal crowding influences progeny size and quantity in desert locust*, Schistocerca gregaria* (Hughes *et al.*, 2003), and at present similar changes in *M. Separata* were observed, the pupal mass of offsprings reared under stressful conditions exhibited a significant decrease, this aligns with the model of population cycle proposed by Steigenga *et al.* (2005) for lepidopteran. Also, the model of Rossiter (1996) suggests that elevated larval densities lead to stress, resulting in lower-quality offspring in the succeeding generation. Similarly, Marshall and Uller (2007) conducted experiments on gypsy moth populations, discovering a correlation between maternal population density and variations in pupal mass, the results of this study demonstrated that egg production was significantly increased, and females who emerged from a high larval population density line laid more eggs, these findings agree with Boggs and Niitepold (2016). During the present study, isolated-reared mothers offspring typically have reduced reproductive potential, similar results were obtained by Uller, (2008). Furthermore, female adult life span was longer at low-density line offspring, these results disagree with the findings of Morag *et al.* (2011), who stated that the longevity of mothers reared at high density was also significantly higher than females reared under low-density conditions reported in a parasitoid wasp. Moreover, high-density females give rise to offspring with quicker development, and these offspring do not experience reduced body size, clutch size, or embryonic survival when compared to offspring of mothers from low-density conditions. These findings suggest that the effects seen in *Copidosoma koehleri* due to high rearing density are not a result of physiological limitations caused by crowding. Instead, they might represent an adaptive reaction to expected competition, through mechanisms distinct from those proposed previously (Morag *et al.*, 2011). Intraspecific competition and food shortage due to high population density during early life stages can profoundly affect adult fitness (Santhi and Trewick, 2022). Remarkable differences were observed in the flight behavior of adults from all offspring treatments; maternal larval density significantly affected the flight potential, including flight duration, distance, and average velocity. When compared to adults that emerged from isolation-reared settings, several butterflies and moths with crowded and food-stressed larvae had lower wing loading, longer forewings, and larger thoracic masses (Jaumann and Snell-Rood, 2019; Rhainds, 2020) such changes can boost flight performance (Tigreros and Da Davidowicz, 2019) and facilitate dispersal from deteriorating habitats. Similarly, offspring whose mothers were reared at moderate and high density displayed the highest, and offsprings raised in isolation had the poorest flight capacity. Maternal larval density also significantly affected the length of the pre-oviposition period; offspring with longer pre-oviposition periods usually showed greater flight potential, and pre-oviposition was positively correlated with flight potential.

Conclusion: It is concluded that the maternal rearing environment (crowding or isolation) strongly impacts the offsprings life history traits, i.e., development period, pupal weight, reproductive plasticity, longevity, and flight performance of respective offsprings in oriental armyworms. Specifically, moderate and high-density reared mothers positively impacted the traits of the next generation.

Authors Contribution: The current manuscript is part of the PhD thesis; the initial idea, data collection, and methodology were initiated by the first author, AWS, with the help of the Supervisory Committee, data analysis, and the current manuscript written by AWS, major supervisor XJ designed experiments of PhD work & guide the scholar. At the same time, YC and LZ contributed to the results and manuscript proofreading.

Acknowledgments: This work was supported by the National Natural Science Foundation of China [Nos. 32072420, 31871951, 31672019], China Agriculture Research System of MOF and MARA [CARS-22], the National Key Research and Development Program of China [2017YFD0201802, 2017YFD0201701], and Beijing Natural Science Foundation [6172030].

REFERENCES

Arbab, A. (2014). Spatial distribution and minimum sample size for overwintering larvae of the rice stem borer, *Chilo suppressalis* (Walker) in paddy fields. Neotrop. Entom. 43: 415- 420. doi:10.1007/s13744-014-0232-y.

Allen, R.M., Y.M. Buckley and D.J. Marshall (2008). Offspring size plasticity in response to intraspecific competition: an adaptive maternal effect across life-history stages. Ameri. Natu. 171: 225-237. doi: 10.1086/524952.

Atkinson, D., S.A. Morley, D. Weetman and R.N. Hughes (2001). Offspring size responses to maternal temperature in ectotherms. In: Atkinson, D., Thorndyke, M. (Eds.), Environment and Animal Development: Genes, Life Histories, Plasticity. BIOS Scient. Publish., Oxford, pp. 269-286.

Benton, T.G., J.J.H. Clair and S.J. Plaistow (2008). Maternal effects mediated by maternal age: from life histories to population dynamics. J. Anim Ecol. 77:1038-1046. doi: 10.1111/j.1365-2656.2008. 01434.x.

Bernardo, J. (1996). Maternal effects in animal ecology. Anim. Zool. 36: 83-105. doi:10.1093/icb/36.2.83.

Boggs, C.L. and K. Niitepold (2016). Effects of larval dietary restriction on adult morphology, with implications for flight and life history. Entomol. Exp. Appl. 159: 189-196. doi: 10.1111/eea.12420.

Dhillon, M.K. and F. Hasan (2018). Consequences of diapause on post-diapause development, reproductive physiology and population growth of *Chilo partellus* (Swinhoe). Physiol. Entomol. 43:196-206. doi: 10.1111/phen.12243.

Ding, Y., C. Sun and B. Dong (2024). Effect of parental rearing styles on adolescent ego identity: the mediating role of evolutionary attitudes. Front. Psychol. 14:1292718. https://doi.org/10.3389/fpsyg.2023.1292718.

Feng, H.Q., K.M. Wu, D.F. Cheng and Y.Y. Guo (2004). Spring migration and summer dispersal of *Loxostege sticticalis* (Lepidoptera: Pyralidae) and other insects observed with radar in Northern China. Environ. Entomol. 33: 1253-1265. doi.org/10.1603/0046-225X- 33.5.1253.

Fox, C.W. and M.E. Czesak (2000). Evolutionary ecology of progeny size in arthropods. Annu. Rev. Entomol. 45: 341-369. doi: .org/10.1146/annurev.ento.45.1.341.

Gibs, M.V., H. Dyck and B. Karlsson (2010). Reproductive plasticity, ovarian dynamics and maternal effects in response to temperature and flight in *Pararge aegeria*. J. Insect Physiol. 56:1275-1283. doi: 10.1016/j.jinsphys.2010.04.009.

Hughes, C.L., J.K. Hill and C. Dytham (2003). Evolutionary trade-offs between reproduction and dispersal in populations at expanding range boundaries. Proc. Res. Soc. Lond. B, 270: S147-S150. doi: 10.1098/rsbl.2003.0049.

Jaumann, S. and C. Snell-Rood (2019). Adult nutritional stress decreases oviposition choosiness and fecundity in female butterflies. Behav. Ecol. 30 (3): 852-863. doi: 10.1093/beheco/arz022.

Jervis, M.A., C.L. Boggs and P.N. Ferns (2005). Egg maturation strategy and its associated trade-offs: A synthesis focusing on Lepidoptera. Ecol. Ent., 56: 145-150. doi: 10.1111/j.0307-6946.2005.00712.x.

Jiang, X., L. Z. Luo and Y. Hu (2000). Influence of rearing temperature on flight and reproductive capacity of adult oriental armyworm, *Mythimna separata* (Walker). Acta Entomol. Sinica. 20: 288-292.

Kendall, B.E., S.P. Ellner, E. McCauley, S.N. Wood, C.J. Briggs, W.W. Murdoch and P. Turchin (2005). Population cycles in the pine looper moth: dynamical tests of mechanistic hypotheses. Ecol. Mono. 75(2): 259-276. doi: 0.1890/03-4056.

Khuhro, N.H., A. Biondi, N. Desneux, L. Zhang, Y. Zhang and H. Chen (2014). Trade-off between flight activity and life-history comoponents in *Chrysoperla sinica*. Bio. Contr. 59: 219-227. doi:10.1007/s10526-014-9560-4.

Kong, H., Y. Zhang, S. Zhu, Y. Kong, L. Wu and R. Hu (2013). Effects of larval density on growth, development and reproduction of diamondback moth (DBM), *Plutella xylostella* L. J. Eco-Agric. 21: 474-479. doi: 10.3390/insects11120857.

Luo, L.Z., B.G. Li, Y.Z. Cao and Y. Hu (1995). The influence of larval rearing density on flight capacity and fecundity of adult oriental armyworm, *Mythimna separata* (Walker). Acta entomol. Sin. 38: 38-45.

Lv, W., L. Zeng, Z. Zhang, H. He, F. Wang and X. Xie (2022). Effects of Juvenile Hormone Analog and Days after Emergence on the Reproduction of oriental armyworm, *Mythimna separata* (Lepidoptera: Noctuidae) Populations. Insec. 13 (6): 506. doi: 10.3390/insects13060506.

Mark, C.E. and J.S. Elkinton (2000). Maternal effects on Gypsy Moth (Lepidoptera: Lymantriidae) population dynamics: a field experiment. Environ. Entomol. 29 (3): 476- 488. doi:10.1603/0046-225X-29.3.476.

Marshall, D.J. and T. Uller (2007). When is a maternal effect adaptive? Oecologia, 116: 1957- 1966. 10.1111/j.2007.0030-1299. 16203.x.

Moore, P.J. and E.W. Harris (2003. Is a decline in offspring quality a necessary consequence of maternal age? Proceedings of the Royal Society of London Series B, Biological Sciences, 270: 192-194. doi: 10.1098/rsbl.2003.0051.

Morag, N., T. Keasar, A. Harari and A. Bouskila (2011). Trans-generational effects of maternal rearing density on offspring development time in a parasitoid wasp. Physio. Entomol. 40: 1-5. doi: 10.1111/j.1365-3032.2011. 00781.x.

Mousseau, T. and C.W. Fox (1998). The adaptive significance of maternal effects. Trends Ecol. Evol., 13: 403-407. doi: 10.1016/s0169-5347(98)01472-4.

Myers, J.H. and J.S. Cory (2013). Population cycles in forest Lepidoptera revisited. Ann. Rev. of Ecol. Evol. and System. 44: 565-592. doi: 10.1146/annurev-ecolsys-110512- 135858.

Palacios, I., O.F. Garcia, M. Alcaide and F. Garcia (2022). Positive parenting style and positive health beyond the authoritative: self, universalism values, and protection against emotional vulnerability from Spanish adolescents and adult children. Front. Psychol. 13:10-16. doi:10.3389/fpsyg.2022.1066282.

Pexton, J. and P.J. Mayhew (2005). Clutch size adjustment, information use and the evolution of gregarious development in parasitoid wasps. Behav. Eco. and Socio. 58: 99-110. doi:10.1007/s00265-004-0881-7.

Rhainds, M. (2020). Variation in wing load of female spruce budworms (Lepidoptera: Tort ricidae) during an outbreak: evidence for phenotypic response to habitat deterioration in collapsing populations. Environ. Entomol. 49: 238-245. doi: 10.1093/ee/nvz144.

Rotem, K., A.A. Agrawal and L. Kott (2003). Parental effects in *Pieris rapae* in response to variation in food quality: adaptive plasticity across generations? Ecol. Entom. 28: 211- 218. doi: 10.1046/j.1365-2311.2003.00507.x.

Rossiter, M.C. (1991). Maternal effects generate variation in life-historyconsequences of egg weight plasticity in the gypsy moth. Func. Ecol. 5: 386-393.

Rossiter, M.C. (1996). Incidence and consequences of inherited environmental effects. Ann. Rev. Ecol. Syst. 27:451-476. doi: org/10.1146/annurev.ecolsys.27.1.451.

Steigenga, M.J., B.J. Zwaan, P.M. Brakefield and K. Fischer (2005). The evolutionary genetics of egg size plasticity in a butterfly. J. Evol. Biol. 18: 281-289. doi:10.1111/j.1420-9101.2004. 00855.x.

Solangi, A.W., L. Zhang, Y. Cheng and J. Xing (2021). Flight affects reproductive performance and offspring development in Oriental armyworm *Mythimna Separata* (Lepidoptera: Noctuidae). Pakistan J. Zool. 53 (3): 913-919. doi: 10.17582/pjz/20180701030740.

Sanghvi, K., F. Zajitschek, M. Iglesias-Carrasco and M.L. Head (2021). Sex- and trait-specific silver-spoon effects of developmental environments, on ageing. Evol. Ecol. 35: 367-385. doi:10.1111/j.0030-1299.2005.13888.x.

Santhi, B. and S.A. Trewick (2022). Effects of population density on adult morphology and life- history traits of female Mediterranean flour moth, *Ephestia kuehniella* (Lepidoptera: Pyralidae). Eur. J. Entomol. 119: 191-200. doi: 10.14411/eje.2022.021.

Tigreros, N. and G. Davidowitz (2019). Flight-fecundity tradeoffs in wing-monomorphic insects. Adv. Insec. Phys. 56: 1-41.

Uller, T. (2008). Developmental plasticity and the evolution of parental effects. Trends Ecol. Evol. 23: 432-438. doi: 10.1016/j.tree.2008.04.005.

Yang, D., X.T. Lai, L. Sun and F.S. Xue (2007). Parental effects: physiological age, mating pattern, and diapause duration on diapause incidence of progeny in the cabbage beetle *Colaphellus bowringi* Baly (Coleoptera: Chrysomelidae). J. Insec. Physio. 53: 900-908.

Yang, F., J.J. Shi and B.P. Zhai (2015). Effects of larval density and food stress on life-history traits of *Cnaphalocrocis medinalis* (Lepidoptera: Pyralidae). J. Appl. Entomol. 139: 370– 380. doi:10.1111/jen.12179.

Xu, R.B., S.S. Ge, W.H. Yu, X.K. Li and K.M. Wu (2023). Physiological and environmental influences on wingbeat frequency of oriental armyworm, *Mythimna separata* (Lepidoptera:

Noctuidae). Environ. Entomol. 52(1): 1-8. doi: 10.1093/ee/nvac101.

Wang, J., X.F. Jiang, D.L. Wu and L.Z. Luo (2008). Effect of larval rearing density on development and fecundity of the beet armyworm, *Spodoptera exempta* (Lepidoptera: Noctuidae). Acta Entomol. Sin. 51: 889-894.

Zhang, L., L. Cheng, J.W. Chapman, T.W. Sappington, J. Liu, Y, Cheng and X. Jiang (2020). Juvenile hormones regulate the shift from migrants to residents in adult oriental armyworm, *Mythimna separata*. Sci. Rep. 10 (1):11626. doi: 10.1038/s41598-020-66973-z.

Zuk, M. and A.M. Stoehr (2002). Immune defense and host life history. Nature. 160: 9-22. doi:10.1086/342131.