



Flight Affects Reproductive Performance and Offspring Development in Oriental Armyworm *Mythimna separata* (Lepidoptera: Noctuidae)

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ABSTRACT

Environment experienced by mothers can influence many of the characteristics of their offspring also apply resource-related maternal effects through differential egg provisioning; we investigated impact of flight on female egg production and longevity in the oriental armyworm *Mythimna separata* (Walker) and whether this contributed to making difference in considered suite of life-history traits on progeny growth i.e. developmental time, larval and pupal mass. We found that forced flight females had early oviposition with higher fecundities and shorter lifespan, whereas control females had delay oviposition with lower fecundities and longer lifespan. In addition, to these maternal effects, flight stimulated changes in maternal egg provisioning had direct significances on progeny life history traits, progeny from forced flight females had poorer larval and pupal masses but development time was extended. However, offspring from control females had heavier larval and pupal masses with shortened development time. It is possible that an increased of flight during the pre-oviposition and oviposition period influence the oviposition trend, egg production and lifespan of the next generation in *M. separata*.

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Authors' Contribution

XFJ designed the experiments. AWS performed the experiments and wrote the article. LZ and YXC analysed the data.

Key words

M. separata, Flight, Maternal effect, Reproductive plasticity, Offspring life history traits.

INTRODUCTION

Maternal conditions can apply resource-related maternal effects through differential egg provisioning, and can significantly influence progeny life history traits (Uller, 2008; Mousseau and Fox, 1998). In insect species, a decline in resources available for reproduction mostly affects the maternal age (Mousseau and Dingle, 1991; Marshall and Uller, 2007; Morag *et al.*, 2011). Flight muscles are the most metabolically active tissue in insects (Harrison and Roberts, 2000) also it (flight) resulted enthusiastically luxurious (Harrison and Roberts, 2000). The oogenesis-flight syndrome hypothesis (Johnson, 1963; Mole and Zera, 1994) forecasts that in flying insect species, physiological constraints caused by an overlap in resources used during flight and during oogenesis results in a resource provisioning trade-off, with rarer resources available for reproductive output (Hughes *et al.*, 2003; Jervis *et al.*, 2005), also female flight performed during oviposition mainly affect the egg size (Gibbs *et al.*, 2005) including adult females whose inspired for flight laid smaller eggs, variation in development time and also affect larval and pupal masses (Gibbs *et al.*, 2010a, b). This proposes the possible for increased flight during

egg laying to make resource-related maternal effects and influence next-generation development (Huang *et al.*, 2005; Gibbs *et al.*, 2010a; Rossiter, 1991). There are good signals in insect species which are predict with regards of life history theory, which propose the deployment of the immune system is energetically expensive and can result in trade-offs with fitness-related behaviors such as; development period larval and pupal masses (Zuk and Stoehr, 2002). The oriental army worm is a nocturnal migratory pest of cereal crops mostly found in Asian countries and Eastern Australia, New Zealand also some Pacific Island with multiple generations per year (Sharma and Sullivan, 2001; Li *et al.*, 1964). The life table of this insect pest is well known in China (Li *et al.*, 1964; Jiang *et al.*, 2014b). Larvae of this polyphagous pest attack on a number of plants including rice, wheat, barley, maize, and sugar cane in China (Zhang *et al.*, 2008a) that annually causes huge crop production and economic losses countrywide (Jiang *et al.*, 2014a). Population dynamics of this noxious species are influenced by many environmental factors (temperature, population, density and flight) (Luo *et al.*, 1995a) from these factors flight is a major factor affecting development, survival rate, and fecundity in *M. separata* (Jiang *et al.*, 2000). Previous studies on *M. separata* flight propose that; after adult emergence within a couple of days migration begins and it mostly occurs pre reproductively (Luo *et al.*, 1996). The female physiological system connected with flight potential,

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flight muscles growth and flight vigor consumption are improved, whereas reproductive systems like; mating, oogenesis, and egg production generally are affected. This condition is overturned after the flight. Consequently, this trend appears to fit the oogenesis-flight syndrome fairly well (Jiang *et al.*, 2000). The objective of our research was to examine whether after an increased flight during the pre-oviposition period and also during female egg laying influence the oviposition trend, egg production and lifespan of forced flight females and no flight females. Later, our interest was to investigate the effects of parent generation (forced flight and no flight mothers) on their offspring biology (development time, larval and pupal mass). We also observed Relationship between reproductive plasticity, longevity, and oviposition period (days) between offspring traits that are forecast to vary in their average level of female flexibility in *Mythmina separata*.

MATERIALS AND METHODS

Stock culture

Eggs were derived from a large outbred laboratory population of *M. Separata* (placed 300-400 individuals per generation) from Institute of Plant protection, CAAS, Beijing, China. Newly hatched larvae (siblings, 10-20 larvae in a 750ml jar) were reared, fresh leaves of maize were provided as diet and were raised till pupa and adult emergence in favorable environmental conditions (Temperature; 24-1-°C; relative humidity; 70%±5 and photoperiod; L14:D10) in insect rearing chamber. After adult emergence we randomly selected 200 females from this laboratory stock and placed separately in netted cages (1m³), having a 2-ml vial with 5% honey solution, a virgin male was allowed to the cage and the mating pair was left undistributed for mating (Jiang *et al.*, 2000; Luo, 1995a).

Maternal treatment (forced flight vs. control)

When females mated successfully were allocated to one of two treatment combination: i) control (no flight) ii) forced flight. Control females placed in their cages without and disturbance or physical pressure and until the first egg was laid, at the first day of oviposition the male was removed from the box and the female was left to continue egg laying up to mortality (Gibbs *et al.*, 2010a). For pilot experiment on day one females from second combinations (forced flight females) were removed from cages and inspired to fly for a short duration of 10 min at optimum temperature (24-1-°C), by gently touching their legs with a fine-bristled paint brush each time they alighted (Gibbs *et al.*, 2010b). When forced flight tested, the females (forced flight females) were brought for copulation in their

cages till the first day of egg laying. When the first egg was laid, the male was removed from the cage and the female was left undisturbed in the cage to continue egg laying. On days 2-4-6 of oviposition, the flight treatment was repeated so that in total each experimental female was forced to fly four times (Gibbs *et al.*, 2010a). A number of female forced to fly were n=20 and control females n=20 experimental females were set up, with five replications of each treatment. After successful mating of these females, they laid viable eggs. Each day, the fresh honeydew solution was provided to mothers of both combinations as adult diet. Daily egg production up to female mortality was counted and considered as total female fecundity (Jiang *et al.*, 2000). Adult life span investigated and calculated as long as the female was alive (Luo *et al.*, 1995a; Jiang *et al.*, 2000).

Offspring development

The intention of the study was to investigate whether maternal regimes affect the considered life history traits of progeny. To control for possible day effects, individual eggs that were laid by females on the same day (day of oviposition) were used to examine offspring performance.

For investigation of offspring life history suites, the eggs laid by mothers from 1st to 8th day of oviposition were added in the analyses. Development time of offspring was investigated for all individuals as an embryonic and post-embryonic development from per combination. For measurements of larval mass (5th and 6th instars) and pupal mass (three-day-old pupae) from all regimes were weighed on an electronic balance (A and D, Tokyo, Japan), and isolated in individual 48 cm³ plastic boxes (Luo *et al.*, 1996; Jiang *et al.*, 2010; Gibbs *et al.*, 2005).

Statistical analysis

For investigation of proposed study, the multivariate equivalent of a t-test the Hotelling's t^2 test (to test mean differences between two groups) was used. This test is same to a multivariate analysis of variance with a two-level factor. In biological terms, this test examines whether both treatment groups are governed by the same kind of trade-offs on a particular day and across days. We used average value from all replicated data of every day, to test the relationship between 'female fecundity, oviposition period and longevity (days)' also 'offspring life history traits' using the Originpro 2015. ANCOVAS were done to determine the influence of maternal treatment (forced flight versus control) and their interaction with offspring development time, larval and pupal masses. Only significant interaction terms were used in the ANCOVA. All statistical procedures performed using through SPSS advanced software (IBM 21 version).

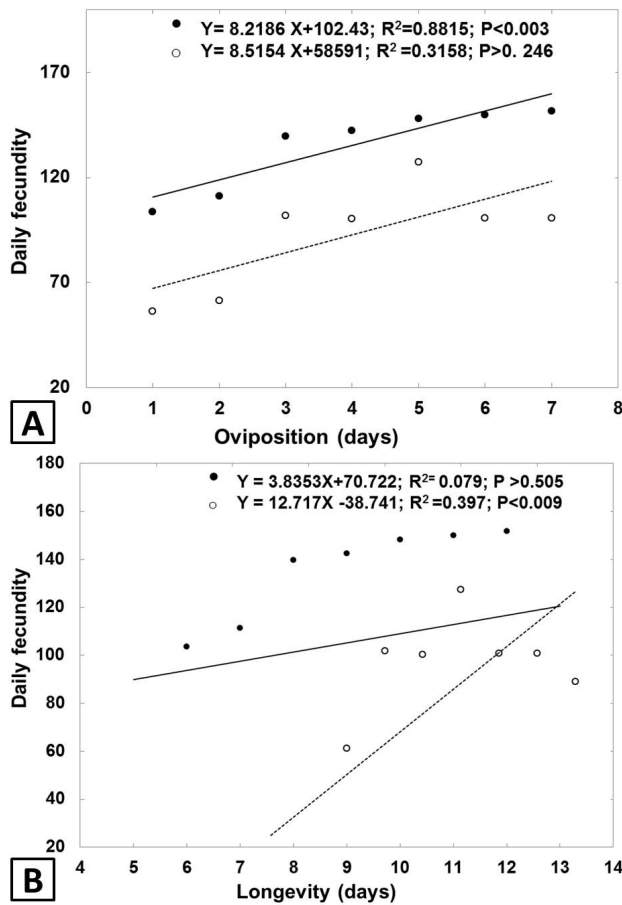


Fig. 1. Regression between daily fecundity and oviposition (days) (A), regression between longevity (days) and mean daily fecundity (B), from the forced flight (filled circle) and control (open circle) in *M. separata* females.

RESULTS

Maternal reproductive plasticity

To examine that control and forced flight females made a significant difference between physiological trade-offs in total numbers of eggs and day of oviposition (1-7 days) were affected by flight. Control and forced flight females displayed a different trend of egg laying at the start of oviposition, at 1st, 2nd and 3rd day of oviposition females from forced flight laid more eggs than control females with significant difference ($t=6.06$; $P<0.0001$). The maximum per day egg production was observed at forced flight than at control females, later they increase egg production from the 4th day of oviposition to onwards, but less than forced flight females. The mothers forced to flight reliably laid more eggs than other mothers on a specific day and across the day. Overall, highest lifetime egg production from forced flight females was recorded than at control

females (mean±S.E, forced flight= 949.68±26.89 eggs, mean±S.E, control= 651.89±35.86 eggs). There was a positive and significant relationship between mean daily fecundity and oviposition period (days) with forced flight mothers, whereas control mothers had and not a significant relationship (Fig. 1A).

Longevity (forced flight and control females)

Adult lifespan showed a significant difference between both treatments; forced fly females had significantly shorter lifespan than control females (mean±S.E, forced flight= 11.06± 0.32 days, mean±S.E, control=12.04±0.27 days). There were significant difference between both treatments ($t=3.13$; $P<0.003$). Relationship between fecundity and longevity (days) from forced flight females were significant and positive, but were negative and not a significant relationship between control females, respectively (Fig. 1B).

Offspring development time

Day of oviposition significantly explained variation in offspring developmental time; Correlation shows eggs from forced females whose laid eggs from 1st to 3rd day, the developmental time was much longer than 4th day to onwards. Whereas, control females lay eggs on 1st to 3rd day of oviposition the developmental time was shortened, but it increases oviposition from 4th to onwards. Overall, mean developmental time was longer at offspring from forced flight and then from control (mean±S.E, forced flight= 44.07± 0.17 days, mean±S.E, control = 42.24 ± 0.21days) with significant differences ($t=6.58$; $P<0.0001$). There was a positive and significant relationship between offspring development time and oviposition (days) from forced flight mothers. Whereas, negative and not a significant relationship between control mothers were observed, as well as significant interaction (Table I; Fig. 2A).

Table I.- Effects of maternal treatment (forced flight and control mothers) on considered life history traits of their offspring in *M. separata*.

Trait / Factor	df	MS	F-ratio	P
Development time				
Maternal treatment	1	15.46	28.83	<0.005
Interaction	1	0.22	16.35	<0.001
Larval weight				
Maternal treatment	1	365.71	13.6	<0.003
Interaction	1	836.65	15.6	<0.002
Pupal weight				
Maternal treatment	1	1547.24	1.57	<0.006
Interaction	1	8618.04	30.80	<0.013

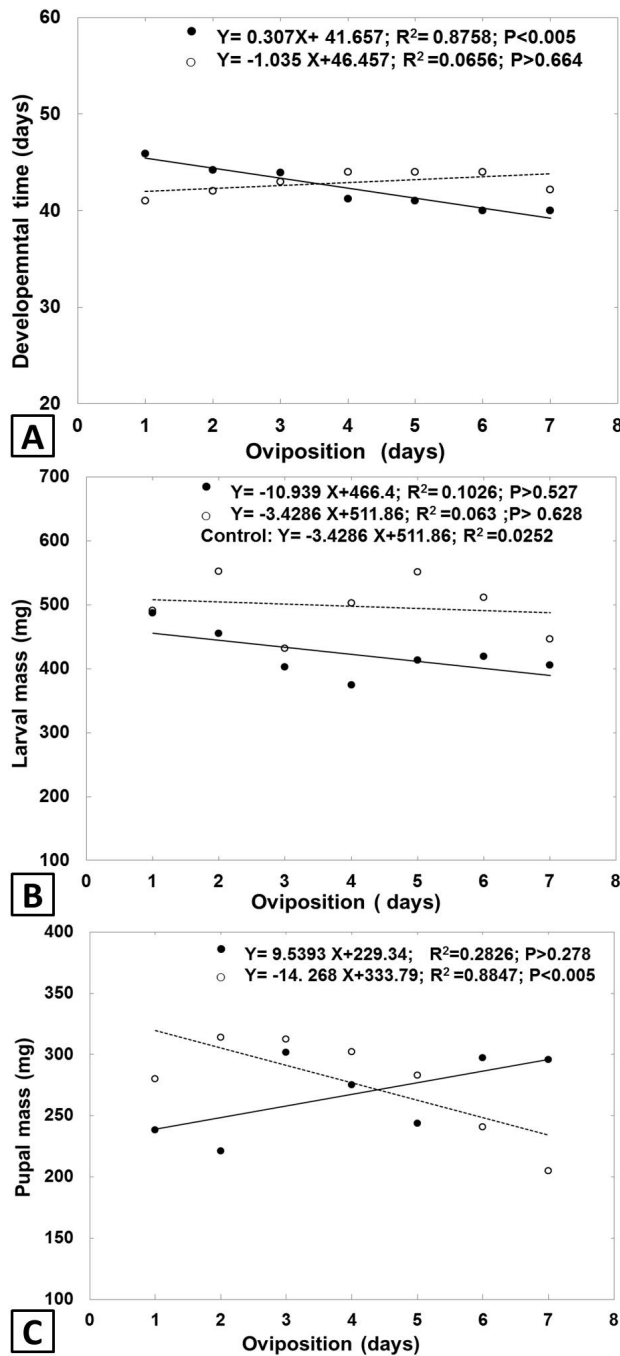


Fig. 2. Regression between offspring development time (days) and oviposition (days) (A), offspring larval mass (mg) and oviposition (days) (B), offspring pupal mass (mg) and oviposition (days) (C) from forced flight (filled circle) and control (open circle) in *M. separata* females.

Offspring larval mass (mg)

Forced flight mothers significantly affect the larval mass (mg) of their offspring; larvae emerged from control

females on 2nd, 4th and 6th day of oviposition significantly heavier. However, larvae hatch from forced flight mothers from 1st and 2nd day of oviposition was heavier, but weight was decreased from 3rd to onwards oviposition days. Overall, larval mass subsequently heavier offspring from a control than at forced flight mothers (mean±S.E, control = 499.37±11.6, mean±S.E, forced flight=424.15±13.18) with significant difference ($t=4.28$; $P<0.001$). It was observed that there was a negative relationship between offspring larval mass (mg) and oviposition (days) from forced flight and control mothers with significant interaction (Table I; Fig. 2B).

Offspring pupal mass (mg)

Pupal mass of offspring was significantly heavier at control than at forced flight mothers (mean±S.E, control = 300.68±4.59, mean±S.E, forced flight= 249.33±5.84), both combinations from 3rd and 4th day of oviposition pupal mass heavier than other days. However, significant difference between both treatments was observed ($t= 6.90$; $P<0.0001$). Correlation shows there were negative but significant relationship between pupal mass and oviposition days from control mothers. Whereas, offspring from forced flight mothers displayed negative and not a significant relationship (Fig. 2C), also significant interactions were observed between both treatments (Table I).

DISCUSSION

The current findings emphasis on physiological trade-offs after flight and reproduction in *M. separata*, and explores the potential for the transmission of flight-induced non-genetic maternal effects. In this study, a substantial intensive flight was performed by females and were stimulated for a flight several times across the oviposition period, as in previous studies flight was performed by a female adult (Gibbs *et al.*, 2010a, b; Hughes *et al.*, 2003, Jervis *et al.*, 2005). We demonstrated that forced flight females displayed highest lifetime egg production on 2nd to 4th day of oviposition (Wiklund and Persson, 1983) and have a significantly maximum egg production, however egg production was dropped with maternal age as previously reported and hypothesized in *P. aegeria* (Gibbs *et al.*, 2010a; Hughes *et al.*, 2003). Pre-oviposition period of *M. separata* females are most sensitive to environmental signals that arbitrate female egg production and can influence adults lifespan, we found forced flight females had early oviposition with higher fecundities and shorter lifespan, whereas control females have delay oviposition with lower fecundities and longer lifespan (Steigenga *et al.*, 2005; Gibbs *et al.*, 2010b). Conflicting to findings on other insect species, we examined that offspring from older

mothers did not differ in survival during the larval stages/ development of offspring (Geister *et al.*, 2008; Gibbs *et al.*, 2010a) development time (Benton *et al.*, 2001) or pupal mass (Rossiter, 1999). Our findings determine that flight significantly affect offspring life history traits, eggs laid by females forced to fly had significantly smaller larval and pupal masses with longer development time (Bernardo, 1996). Whereas, offspring from control females had shorter developmental time with heavier larval and pupal masses, this variation in results shows the potential for flight-induced changes in maternal egg provisioning to continue applying effects later in progeny growth (Gibbs *et al.*, 2010a, b). The forced flight period appears very short, as compared with field or laboratory tethered flight evaluations from previous studies of a female was tested in *M. separata* by Jiang and Luo (2005), Li and Luo (1999) and Jiang *et al.* (2005). What we found, although lowest flight duration during egg-laying may influence female egg production, longevity and offspring performance (Benton *et al.*, 2005). Moreover, during the flight, females want to take landing and rest but continue to push up repetition for flight and avoid landing it is most energetically expensive kind of acceleration (Mark *et al.*, 2000). This study revealed that; flight duration and nature of flight test (after adult emergence) together apply a significant influence on offspring fitness. Marshall and Uller (2007) also reported a current analysis cautioned against using 'snapshot' experimental studies to examine whether changes in maternal investment in offspring may have an adaptive significance. Also, our findings obviously expose the cross-generational effect and highlight the significance for the establishment of several behaviors in new findings, because the effects are most probably trait-related. During our findings, *M. seaprata* flights negatively influence on offspring life history traits. For this noxious insect pest, this study is the first to prove that flight before and during egg-laying may influence mothers lifetime egg production as well as the progeny growth.

CONCLUSION

It is concluded that flight performed before or during female egg-laying may apply maternal fitness effect in *M. separata*. Also, it was observed characteristics of the progeny affected by the maternal environment in our study. This could have important consequences for population dynamics, mostly in agricultural fields. *M. separata* has fascinated attention in studies of distribution and dispersal in response to climate changes, and in studies of evolutionary trade-offs at both increasing range margins and in relation to habitat fragmentation.

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Statement of conflict of interest

The authors declare no conflict of interest.

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