

## Effects of parental exposure to high temperature on offspring performance in the cotton bollworm, *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae): adaptive significance of the summer diapause

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### Abstract

Summer diapause in the cotton bollworm, *Helicoverpa armigera* (Hübner), is prolongation of the pupal stage, particularly in males, induced by high temperatures. The effects of exposing a parental generation to temperatures of 33 to 39°C on the development, survivorship, longevity and fecundity of their offspring were determined in the laboratory. Three groups of offspring were examined: A, the progeny of control female moths reared as larvae at 27°C mated to male moths that had undergone summer diapause when exposed to high temperature; B, the progeny of control female moths mated to males that had not undergone summer diapause after exposure to high temperature; C, the progeny of control females mated to control males reared at 27°C. The developmental times of the immature stages were significantly different between groups. The survival rate in the immature stages varied significantly from 69.8% (Group C) to 34.7% (Group B). The average number of eggs produced per female and the longevity of females and males were not significantly different. The indices of population increase of Groups C, A and B were 286.2, 256.8 and 145.0, respectively. These results indicate that Group A offspring had physiological advantages, such as survival and population increase, compared to Group B offspring. The adaptive significance of summer diapause in the cotton bollworm is discussed in relation to the performance of offspring.

**Key words:** *Helicoverpa armigera*; summer diapause; development and survivorship; index of population increase

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### INTRODUCTION

The cotton bollworm, *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae), is widely distributed throughout the Old World and is a serious pest attacking various crops, including cotton, corn, tobacco, hot pepper, tomato and kidney beans. In China, this species has four or five generations a year in most areas and overwinters as diapause pupae in soil. The biology and ecology of *H. armigera* have been described in detail (Zalucki et al., 1986, 1994; Fitt, 1989). Previously, the effects of pre-winter and winter temperatures and daylength on the induction, maintenance and termination of winter diapause have been studied (Kuznetsova, 1972; Wilson et al., 1979; Wu and Guo, 1995).

Summer diapause (aestivation) is a kind of developmental rest by which insects avoid hyperthermia and other associated physiological stresses (dehydration, starvation) (Ushatinskaya, 1987). It is also an important mechanism for the synchronization of life cycle with the growing season by avoiding unfavorable environmental conditions (Beck, 1980; Xue et al., 1997). There have, however, been few studies on the ecological performance of this species at high temperature (Hackett and Gatehouse, 1982; Nibouche, 1998). Butler et al. (1985) discovered that *Heliothis virescens* underwent summer diapause at temperatures above 32°C. This led to a speculation that *H. armigera* might also undergo a similar diapause. However, evidence for summer diapause in *H. armigera* was lacking until Nibouche (1998) described a “hot thermal dia-

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pause” initiated at 37°C in a population from tropical Burkina Faso. In China, summer diapause in the cotton bollworm has been demonstrated (Wu and Gong, 2000). It is induced by high temperature. The sensitive stage is the prepupa and the critical temperature is 33°C.

The adaptive significance of winter diapause in *H. armigera* is obvious since this allows pupae to survive otherwise lethal winter temperatures (Wilson et al., 1979). However, the adaptive significance of summer diapause in the cotton bollworm remains unclear. The host plants of the pest may not be limited in summer, and the only environmental factor inducing summer diapause is high temperature (Wu and Gong, 2000). The male moths are sensitive to high temperature, producing malformed spermatozoa (Guerra, 1972; Wang et al., 1996). In most temperate parts of China, the hottest time is late July and early August. The daily maximum temperature is nearly 40°C and the temperature of the soil surface may reach 50°C. Such a high temperature may be deleterious and the cotton bollworm may avoid hyperthermia by entering summer diapause. It is possible that summer diapause in the cotton bollworm can confer benefits to the offspring. Butler et al. (1985) found some evidence for such benefits in the tobacco budworm.

However, there has been no detailed research on the effect of summer diapause on the performance of the offspring. We investigated this problem in the cotton bollworm, discussing the adaptive significance of summer diapause in terms of development, survivorship, longevity, fecundity and other parameters in the offspring.

## MATERIALS AND METHODS

**Establishing a laboratory colony.** A laboratory colony of *H. armigera* was established by collecting full-grown larvae from cotton in the suburbs of Beijing. The larvae were reared on an artificial diet (Wu and Gong, 1997) at 27°C with a photoperiod of LD14:10 to prevent winter diapause. Newly hatched larvae were reared in groups until the 3rd instar, after which they were separated in individual glass tubes (2.0 cm dia.×8.0 cm high) to prevent cannibalism. Mature caterpillars were allowed to pupate in moist soil with a water content of about 7%. Emerged moths were allowed to mate in cages (50 cm length×50 cm width×50 cm high) for

three days, and were provided with 10% sucrose solution.

**Criteria for summer diapause.** Two characteristics were used to determine whether or not pupae were in diapause. The first was the retention of pigmented eye spots in the postgenal region (Shumakov and Yakhimovich, 1955). These disappear during the first two days of pupation (mean<1.6 days) at temperatures  $\geq 30^\circ\text{C}$  in non-diapausing pupae (Wu and Gong, 2000). Irrespective of temperature, pupae showing these eye spots for four days after pupation were considered to be diapausing. The second characteristic was the condition of the fat body in the pupal abdomen (Pearson, 1958). The fat body of newly formed pupae is composed of firm rounded lobes and remains unchanged throughout diapause. Its histolysis coincides with movement of the eye spots and is therefore a valid supplementary criterion.

**Experimental designs.** Summer diapause in the cotton bollworm occurs mainly in males and the incidence of summer diapause in the female is very low (Wu and Gong, 2000). Thus, diapausing females are very difficult to obtain. Considering these conditions, three groups of offspring were examined in our experiments: Group A, the progeny of male *H. armigera* moths from diapause pupae that had been exposed to daily cycles of 33°C (16 h mainly in the scotophase) and 39°C (8 h in the photophase) as prepupae were crossed with control female moths reared from larvae maintained at 27°C; Group B, the progeny of male moths from non-diapause pupae reared as in the above group were crossed with control female moths kept at 27°C; and Group C, the progeny of control male moths mated to control female moths both obtained at 27°C. The effects of a male parent’s summer diapause on the performance of their offspring, the development and survivorship of immature stages, adult longevity and reproduction, and the index of population increase in terms of performance of offspring of each group were determined.

**Induction of diapause by high temperature.** Larvae were reared to the final larval stage at 27°C and LD14:10, then prepupae were transferred to a temperature regime of 33 to 39°C, the higher temperature for 8 h in the photophase and the lower temperature for 16 h in the scotophase. Prepupae were allowed to pupate in moist soil (water 7%) to induce summer diapause (80 larvae each of five

replicates), and the incidence of diapause and the retention of eye spot in non-diapause pupae were recorded. After emergence of the non-diapause pupae at 33–39°C, the diapause pupae were transferred to 27°C, and the retention of eye spots was recorded. At the same time, control pupae (from larvae reared at 27°C) were checked and the retention of eye spots were recorded.

**Development and survivorship of immature stages of offspring.** All moths from the same group were mated in a mating cage (50 cm length×50 cm width×50 cm high) for two days and then transferred to an oviposition cage (25 cm length×25 cm width×25 cm high) equipped with a plastic window screen fixed with thumb pins as an egg laying substratum. This may prevent eggs being laid on the cage wall. The moths were supplied with 10% sucrose solution as food. The sheet of window screen with the eggs was cut into small pieces and 40 eggs laid on the same day in each group were taken to determine the hatching rate (30 replicates). Egg survivorship was calculated as the number of hatched eggs divided by the total number of eggs. Eggs laid on the same day of each group were kept in separate jars (12 cm diameter×7.0 cm high). Three hundred newly hatched larvae of each group were reared individually in each glass tube to prevent cannibalism, provided with an artificial diet, at 27°C under a photoperiod of LD14:10. Individual insects were checked twice a day for ecdysis to determine the durations of life stages and survivorship. The cast head capsules were used to determine moulting. Mature larvae were allowed to pupate in moist soil (water content of about 7%). The pupal weight was measured two days later. Pupal weight, larval and pupal periods, and percentages of individuals pupating and emerging as adults were recorded.

**Adult longevity and reproduction of offspring.** All emerged moths in the same group were mated in a mating cage for two days, then transferred to oviposition containers (8 cm diameter×10 cm high) (one pair per container with no fewer than 30 replicates) each with a window screen for egg laying, and 10% sucrose solution as food. After the initiation of reproduction, adult mortality and numbers of deposited eggs were recorded daily. The dead female moths were dissected to determine the number of eggs remaining in the body cavity and the presence of spermatophores.

## RESULTS

### Characteristics of summer diapause of *H. armigera*

Prepupae are sensitive to high temperatures: the higher the temperature, the higher the incidence of diapause (Wu and Gong, 2000). The exposure to the alternating temperature of 33–39°C caused an average of 63.2% of males and 10.9% of females to enter summer diapause. The incidence of summer diapause in males was significantly higher than in females ( $t=7.049$ ;  $df=8$ ;  $p<0.001$ , arcsine transformed; 80 larvae each of 5 replicates).

When diapausing pupae were transferred to 27°C from 33–39°C, about 10 days was required to terminate diapause compared with non-diapausing and control pupae, which lost their eyespots in 1–2 days, showing a significant difference ( $F=160.90$ ;  $df=2, 289$ ;  $p=0.001$ ; Scheffé's test).

### Development of offspring

There were significant differences in developmental time of the immature stages between Groups (Table 1, Scheffé's test). Group C developed significantly faster than Group A or B and Group A had a significantly longer developmental time (30.2 d) than Group B (25.9 d).

Differences in pupal weight between groups were pronounced (Fig. 1). Group C had the heaviest pupal weight, followed by Group A, and then Group B. Although the pupal weights of both males and females in group A were larger than in Group B, the differences were not significant.

### Survivorship of immature stages of offspring

Egg hatching was significantly affected by parental diapause. Although egg hatching in Groups C ( $88.6\pm5.8\%$ ) and A ( $87.3\pm6.8\%$ ) were not significantly different, both were significantly higher than in Group B ( $79.0\pm10.5\%$ ) (Fig. 2; Scheffé's test after arcsine transformation). There were also considerable differences in survival of immature stages among Groups C, A and B (69.8, 54.5 and 34.7%, respectively) (Table 2,  $\chi^2=41.12$ ;  $p<0.0001$ ). Heavy mortality occurred at early stages, and there were significant differences among the three groups (Table 2).

Table 1. Developmental periods (d) of immature stages in offsprings of *H. armigera*<sup>a</sup>

Stage	Group A	Group B	Group C
Egg	3.00±0 a	3.00±0 a	3.00±0 a
1st stage	2.40±0.07 (170) a	2.24±0.05 (182) a	2.27±0.04 (192) a
2nd stage	2.91±0.11 (164) a	2.42±0.05 (181) b	2.18±0.05 (188) b
3rd stage	2.28±0.08 (164) a	2.04±0.02 (173) b	1.97±0.05 (188) b
4th stage	2.58±0.08 (161) a	2.09±0.06 (173) b	2.05±0.04 (187) b
5th stage	2.35±0.07 ( 95) a	1.77±0.05 ( 75) b	1.33±0.07 ( 73) c
6th stage	2.93±0.05 (159) a	2.53±0.05 (172) b	1.84±0.04 (185) c
Prepupa	2.67±0.06 (157) a	2.40±0.05 (167) b	1.64±0.03 (183) c
Pupa	10.76±0.07 (149) a	8.86±0.05 (152) b	8.52±0.05 (180) c
Combined stage	30.24±0.21 (149) a	25.91±0.12 (152) b	23.96±0.15 (180) c

<sup>a</sup>Data are shown as means±SE and numbers in parentheses are samples sizes. Values within a row followed by different letters are significantly different at  $p\leq 0.05$  (Scheffé's test). Group A, the progeny of control female moths reared as larvae at 27°C mated to male moths that had undergone summer diapause when exposed to high temperature; Group B, the progeny of control female moths mated to males that had not undergone summer diapause after exposure to high temperature; and Group C, the progeny of control females mated to control males reared at 27°C. Groups A, B and C were the same meaning in the following tables.

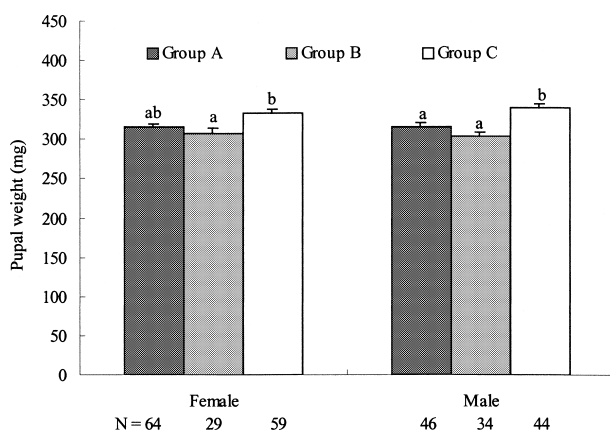


Fig. 1. Pupal weight (mean±SE) of progeny of *H. armigera*. N indicates samples sizes. The same letter above bars indicates that means were not significantly different at  $p\leq 0.05$  (Scheffé's test). Group A, the progeny of control female moths reared as larvae at 27°C mated to male moths that had undergone summer diapause when exposed to high temperature; Group B, the progeny of control female moths mated to males that had not undergone summer diapause after exposure to high temperature; and Group C, the progeny of control females mated to control males reared at 27°C.

### Adult longevity and fecundity of female adults of offspring

The results are shown in Table 3. There were no significant differences in the longevity of female and male adults between groups (Table 3), suggesting that paternal diapause did not influence the longevity of offspring, while the fecundity was affected. Although the number of eggs laid was not

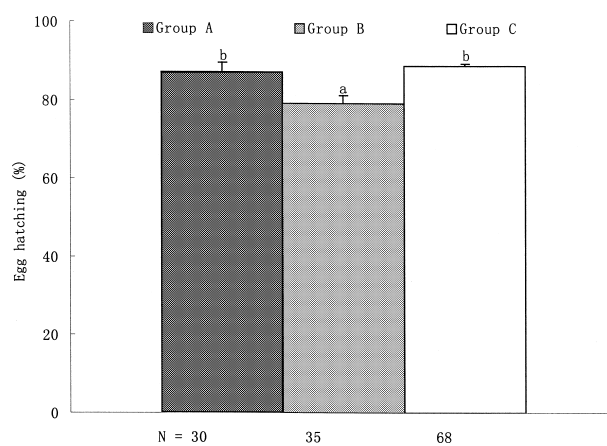


Fig. 2. Egg hatching (mean±SE) of progeny of *H. armigera*. N indicates samples sizes. The same letter above bars indicates that means were not significantly different at  $p\leq 0.05$  (Scheffé's test). See above for application of Groups A, B, C.

significantly different, the number of eggs remaining in the female body cavity and the percentage of eggs laid were significantly different among the three groups (Table 3). The index of population trend (Morris and Fulton, 1970) of Group C was the highest (286.2), followed by Group A (256.8) and Group B (145.0) (Table 3). Group A had a higher fitness than Group B because of a greater for capacity population increase than that of Group B.

Table 2. Survivorship (%) of immature stages for offsprings of *H. armigera*<sup>a</sup>

Stage	Group A	Group B	Group C	Chi-square	<i>p</i>
1st stage	69.4 (245) b	57.5 (316) c	84.5 (227) a	45.1428	<0.0001***
2nd stage	96.5 (170) a	87.5 (203) b	97.9 (192) a	20.7500	<0.0001***
3rd stage	100.0 (164)	98.9 (180)	99.5 (188)	3.9259	0.1644
4th stage	99.4 (164)	100.0 (178)	100.0 (188)	3.9847	0.1364
5th stage	97.9 (97)	100.0 (76)	98.6 (74)	1.5263	0.4662
6th stage	98.8 (161)	99.4 (172)	98.9 (187)	0.4176	0.8118
Prepupa	98.7 (159)	97.1 (171)	98.9 (185)	2.0789	0.3536
Pupa	97.5 (157)	96.8 (166)	98.4 (183)	5.8900	0.3171
Combined stage	54.5 (245) a	34.7 (316) b	69.8 (227) a	41.1210	<0.0001***

<sup>a</sup> Numbers in parentheses are samples sizes. Values within a row followed by different letters are significantly different at  $p \leq 0.05$  (Chi-square test).

\*\*\* significant at  $p \leq 0.0001$  (Chi-square test).

Table 3. Fecundity of female adults in the offspring of *H. armigera*<sup>a</sup>

	Group A	Group B	Group C
Adult longevity			
Female	7.9±0.3 (64) a	8.1±0.3 (40) a	7.8±0.4 (50) a
Male	10.3±0.6 (62) a	10.7±0.4 (33) a	9.7±0.5 (47) a
Number of eggs laid	941.8±66.6 (73) a	834.9±64.3 (60) a	820.3±46.9 (81) a
Number of remaining eggs	38.5±15.5 (73) a	103.7±19.6 (58) b	59.9±6.1 (86) a
% egg laid	89.1±2.0 (68) ab	81.5±3.2 (55) b	89.7±1.6 (81) a
% mated <sup>b</sup>	65.0±5.4 (58)	63.0±5.3 (91)	66.0±4.9 (73)
Survival rate of generation (%)	54.6	34.7	69.8
The index of population increase	256.8	145.0	286.2

<sup>a</sup> Data are shown as means±SE and numbers in parentheses are samples sizes. Values within a row followed by different letters are significantly different at  $p \leq 0.05$  (Scheffé's test).

<sup>b</sup> No significant differences ( $\chi^2=0.33, p>0.05$ ).

## DISCUSSION

Summer diapause may be defined as diapause induced before the height of summer, and terminated and followed by reproductive, developmental, or feeding activities in autumn or winter (Masaki, 1980). Summer diapause is an adaptive mechanism to cope with unfavourable environmental conditions and to synchronize emergence with the next favourable season.

Tombes (1964) pointed out that summer diapause existed in both male and female insects and had four characteristics, i.e., low water content, low respiratory rate, high lipid content and undeveloped reproductive organs. Summer diapause of the cotton bollworm induced by high temperatures above 33°C was prolongation of the pupal stage. Only a portion of individuals of this insect enter

summer diapause and more males than females do so at high temperatures. This tendency is similar to that previously reported (Denlinger, 1981; Butler et al., 1985). The duration of diapause was long enough to pass the hot season. The diapausing pupae can persist one month or more and 20% of them can survive two months at 35°C (Wu and Gong, 2000). When transferred to 27°C, the diapausing pupae did not terminate their diapause immediately and required a period of about 10 days to terminate diapause. The dormancy described here can be regarded as summer diapause, but not "hot thermal quiescence".

In summer, the larvae mainly developing on agricultural crops, such as cotton, are often subjected to hot and dry conditions, especially during the prepupal stage in the soil. Such conditions probably serve as a cue to enter summer diapause.

In China, the temperature in late July and early August is very high, sometimes reaching 40°C, which is high enough to induce diapause. If the temperature has been high and a substantial number of insects has entered diapause during summer, adult populations of the cotton bollworm may be relatively small during late July and early August. However, in late August, large populations of cotton bollworm adults often appear in Xinjiang Autonomous Area of China (Guo, 1998) and, based on our results, we presume them to be from summer diapause pupae. This paper is the first to explore the effects of paternal diapause in response to high temperature on the performance of offspring.

Our results show that the developmental time of immature stages whose male parents entered summer diapause in response to high temperature was longer than that of the progeny of males that did not enter summer diapause (Table 1). In general, quicker development of larvae means a higher fitness. However, under special conditions such as a spell of hot weather after the beginning of autumn in China, the slower development of larvae may be responsible for protecting high temperature-sensitive pupae in the hot season. There may be various mechanisms affecting the performance of the progeny whose paternal parent entered summer diapause. One might be an adverse effect of heat. Exposure of *H. armigera* to high temperature during the nondiapause pupal stage may reduce the fertility of male moths by decreasing the viability of sperm, as indicated by the lowered rate of egg hatch. Male pupae that enter summer diapause may be able to avoid this reduction in fertility. In our results the progeny of Group A were the slowest to pupate and emerge as adults which may cause pupae of offspring to escape from high temperature thereby potentially reducing the risk of sperm damage. On the contrary, the progeny of Group B lack the ability to delay development and their fertility is reduced.

Pupal weight can be an indirect, but easily measured, indicator of fitness in Lepidoptera (Leuck and Perkins, 1972). The pupal weights both of male and female in Group A were heavier than in Group B, although the differences were not significant. The survivorship of immature stages also showed similar differences. Fifty-four point five percent of the offspring of the males (Group A) that had entered summer diapause survived to

adulthood, compared to only 34.7% of those produced by the males (Group B) that did not diapause at high temperature (Table 2). These results suggest that Group A progeny had better adaptive capability compared to Group B. The effects of exposure of the male parent to the high temperature were manifested in the early stages of offspring.

Although there were no significant differences in longevity between female and male adults, fertility was significantly different among the three groups (Table 3). There might be several factors affecting fecundity, including temperature, growth and development in the larval stage, adult body size and feeding, the quality of mated female moths and the male's nutritional contribution. In our experiment, the environmental conditions of offspring were the same, the causes for their different performances may be ascribed to whether or not the male parent experiencing high temperatures and summer diapause.

The index of population increase, an important indicator of population dynamics (Morris and Fulton, 1970), is a key statistic that adequately summarizes the physiological capacity for increase. We computed it from the data of egg hatching rate, survival rate of immature stages, and egg production. It was 257 in Group A, but only 145 in Group B, indicating that the progeny of males that entered summer diapause had greater capability for population increase than those of males that did not.

Our results showed there were significant differences between the offspring of diapaused and nondiapaused male parents at high temperature. Besides the environmental factor (high temperature) and experience (diapause or not) in the parent, genetic differences may also be attributed to these. do Nascimento et al. (2002) did reported genetic components affected development time in *Drosophila melanogaster*. However, our understanding of the molecular regulation of diapause remains in its infancy (Denlinger, 2002). How the male parent can influence the progeny's fitness remains a fascinating question and deserves further research.

We conclude that summer diapause is a mechanism in the cotton bollworm that confers advantage on the offspring. In addition to these, summer diapause itself has its own adaptive significance. It is maintained by high temperatures during summer and rapidly broken by falling temperatures, which can synchronize the emergence of adults to occur

in autumn serving as an negative feedback system to stabilize the seasonal life cycle. In *H. armigera*, a portion of the population lies dormant during the period of high temperature but the rest continue to develop. The possible consequence of this is similar to other types of polymodal emergence strategy, which have been described as “bet hedging” (Waldbauer, 1978) against unpredictable risks due to a fluctuating environment.

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