

Effect of body size and larval experience on mate preference in *Helicoverpa armigera* (Hübner) (Lep., Noctuidae)

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Abstract: We studied the mating selection in the cotton bollworm, *Helicoverpa armigera* (Hübner), in relation to body size and larval diet in the laboratory. When provided with an artificial diet at larval stage, weight, body and forewing length did not affect the probability of a male/female moth being selected for mating, but the abdominal width of selected female moths was significantly wider than that of non-selected female moths. 30 female moths were dissected and number of eggs was counted after mating, and there was a correlation between the abdominal width and egg number. There was also significant difference of weight loss between selected and non-selected male/female moths after the mating. The effect of operational sex ratio on mating latency and copulation duration were tested, and the result indicated that mating latency of male selection was significantly longer than that of female selection, but the difference of copulation duration was not significant. Cotton, corn and peanut plants were provided to larvae to test the effect of larval host plant experience on mate choice. When cotton- and peanut-fed moth served as potential partners, both female and male of cotton-fed moths significantly preferred cotton- to peanut-fed moths for mating. The possible reasons for mate preference based on larval host plant experience may account for host plants attributes on sex pheromone variation and sexual maturity. These findings may impact *Bacillus thuringiensis* resistance management.

Key words: *Helicoverpa armigera*, body size, larval host, mate selection, mating latency

1 Introduction

Mate choice, an important component of sexual selection (VAN DONGEN et al., 1997), was defined by HALLIDAY (1983) as any pattern of behaviour shown by members of one sex, which leads to them being more likely to mate with certain members of the opposite sex than with others. Non-random mating is of fundamental evolutionary importance because different matings may have different fitness consequences, causing evolutionary changes in morphological and behavioural characters (SVENSSON, 1996). It also possesses practical applications to integrated pest resistance management, especially for the high-dose/mixture strategy in resistant pest management, which assumes random mating between the resistant and susceptible individuals (KLEPETKA and GOULD, 1996). Important factors of mating selection for moths mainly involve body size, age, virginity, larval and/or adult diet, and others (SVENSSON, 1996), and at least three major forms of general mate assessment strategies (best of N rule, threshold-comparison rule, best of all rule) that have been proposed for mate selection (SVENSSON, 1996; JIMÉNEZ-PÉREZ and WANG, 2004). Recent studies also revealed the paternal inheritance of female mating preference in the arctiid moth *Utetheisa ornatrix*,

which may be common in the Lepidoptera (IYENGAR et al., 2002). Operational sex ration (OSR; EMLÉN and ORING, 1977) and choosiness appear to be related because the underrepresented sex may afford to be selective without losing the mating opportunities (VAN DONGEN et al., 1997). Combined with intrasexual competition, mating latency (time from a first encounter between a male and a female until copulation) may vary with different OSR. If it is related with mate guarding, OSR could also affect copulation duration.

Helicoverpa armigera (Hübner) (Lep., Noctuidae) is a widespread polyphagous pest of many agricultural and horticultural crops (ZALUCKI et al., 1986; FITT, 1989) that can complete 3–4 generations each year in north China. The first generation is on wheat, and the major host plants for the second to fourth generations mainly include cotton, corn, peanut, soya bean, and other plants, and comprise ≈14 million hectare in the proportion of 5, 55, 15, 15 and 10, respectively (WU et al., 2002), the pattern of which is a continuous random mosaic. Different host plants are known to affect the insect development, survivorship, reproduction and life table parameters (TSAI and WANG, 2001; KIM and LEE, 2002). For *H. armigera*, body weight and development were significantly affected by host plants

(LIU et al., 2004). If morphologic characters or/and development based on larval diet possess affects on mating preference, then host plants can result in assortative mating indirectly.

Moreover, random mating between susceptible and resistant individuals is the key factor in the application of refuges in the agrosystem with transgenic *Bacillus thuringiensis* (*Bt*) crops (McGAUGHEY and WHALON, 1992; KLEPETKA and GOULD, 1996; ENVIRONMENTAL PROTECTION AGENCY, 1998; GOULD, 1998). In northern China, corn or peanut usually served as refuge crops. If there are assortative matings between the different host races, the refuge function of these crops will be invalidated. This study was conducted to determine if there are any effects of body size and larval diet on mating selection for both sexes of *H. armigera*.

2 Materials and Methods

2.1 Insect rearing and experimental conditions

A laboratory population of *H. armigera* was established by collecting full-grown larvae from a cotton field in Raoyang County, Hebei province. Larvae were continuously fed a wheat-germ artificial diet (WU and GONG, 1997) for eight generations before testing at 27°C with a reverse photoperiod of 14 : 10 (L:D)hours (lights off at 0900 hours) and ambient conditions of relative humidity of 60 ± 3%. Thirty female and thirty male pupae were randomly collected and placed in separate 15 cm petri dishes. Emerged adults moths were provided a 10% sucrose solution and allowed to mate for 2 days in cages (50 cm length × 50 cm width × 50 cm high). Mated moths were transferred to egg laying containers (25 cm length × 25 cm width × 25 cm high) with nylon gauze for oviposition. Eggs were collected continuously for 3 days in separate glass jars (12 cm dia. × 7.0 cm high) without regard to the mating pair. Newly hatched larvae were reared in groups until the second instar, after which they were separated in individual glass tubes (2.0 cm diam. × 8.0 cm high) to prevent cannibalism. To test the effect of adult size on mate choice, no fewer than 800 larvae were provided with the artificial diet. To test the effect of host plant species on mate choice, the following three crop plants commonly found in north China were used as food at larval stage: cotton (*Gossypium hirsutum* L.), corn (*Zea mays* L.), and peanut (*Arachis hypogaea* L.). All plant materials used in this experiment were collected from the plants growing under field conditions without pesticides. Plants were fertilized with a controlled release fertilizer and watered as required. No fewer than 400 larvae per host plant species were provided with tender leaves changed every day until the third instar, after which larvae were given fruits of host plants except those reared on peanut, which continued to feed on leaves until pupation.

Mature caterpillars were allowed to pupate in a moist soil substratum with a water content of about 7% (soil was heated at temperature 120°C for 2 h and sifted through sieve with 36 apertures per cm²). Pupae were separated by sex and kept individually until adult emergence to ensure virginity. Every day, 4 h into scotophase, moths in the emergence cages were moved to empty cages according to sex and emergence date, and fed a 10% sucrose solution. The emergence date of moths was recorded and moths on the scotophase of emergence were designated as 0 day. Most females start calling on the second or third day following the emergence (KOU and CHOW, 1987;

HOU and SHENG, 2000), so we took 3-day-old virgin moths as the object of study for all experiments.

2.2 Influence of body size on mate selection

We tested the hypothesis that females and male choose partners based on their body size and mass. All adults were weighed using a Mettler electronic scale (0.1 mg accuracy, Type AE 200, Mettler, Switzerland) before tests and randomly placed in cages (50 cm length × 50 cm width × 50 cm high) for a male/female moth and two female/male moths. The time that moths were placed in cage and the time of initiation and completion of mating were recorded. After the experiments, moths were anaesthetized, and the body weight and morphological characters were measured. In male and female choice experiments, the length of the body and wing (from base to distal tip) for selected and non-selected moths was measured using a vernier caliper. In male choice experiments, the abdominal width of selected and non-selected females was measured under a dissecting microscope (Olympus, Tokyo, Japan) with an ocular micrometer; a total of 68 males and 133 females were used as selectors. Another 30 pairs of 3-day-old virgin moths were used to test the correlation between abdominal width and number of eggs. After mating, the female was dissected and eggs were counted.

2.3 Influence of host plant at larval stage on mate selection

The objective of this experiment was to determine whether males and females discriminated partners based on their larval diet. There were two combinations of mating selection based on larval diet for male and female moths: mating choice between individual fed on cotton and individual fed on corn, mating choice between individual fed on cotton and individual fed on peanut. We performed more than 50 replicates for both female and male selectors. For replicate of each combination, we released a virgin moth from one host (selector) and two virgin potential partners (one for each host) to the arena and observed the selection behaviour for mates. The combination is as follows:

Selectors	Partner	
	Peanut	Cotton
Peanut		
♂	♀	♀
♀	♂	♂
Cotton		
♂	♀	♀
♀	♂	♂
	Corn	Cotton
Corn		
♂	♀	♀
♀	♂	♂
Cotton		
♂	♀	♀
♀	♂	♂

2.4 Statistical analysis

Statistical analyses were performed using SAS Stat (SAS Institute Inc, 1988) and P < 0.05 was set as the rejection level. To test whether insects selected their partners based

on body mass and several morphologic parameters, we compared the mean value of characters of selected and non-selected by a paired *t*-test. Pearson's correlation test was performed to estimate the correlation of female abdominal width and egg number. Mating latency and copulation duration for male and female selector were tested by Wilcoxon–Mann–Whitney test. Student's *t*-tests were conducted to compare weight loss of selected and non-selected moths. To test whether insects selected their partners based on larval host plant experience, we used a binomial test.

3 Results

3.1 Influence of body size on mate selection

Length of body and forewing, body weight of *H. armigera* did not affect the probability of being chosen for mating of both male and female. The abdomen of selected females was wider than that of non-selected females, and correlation test also showed that there was a positive correlation between abdominal width of female moth and egg number (table 1, fig. 1).

The weight loss of selected female was significantly less than that of non-selected female moths, and the weight loss of selected male was significantly more than that of non-selected male moths (table 1, fig. 2).

Mating latency and copulation duration distribution for male and female selector show that mating latency of male selection was significantly longer than those of female, but the difference of copulation duration between male and female selection is not significant (table 2, fig. 3).

3.2 Influence of larval host on mate selection

For selection experiments between larvae fed on cotton and peanut, cotton-fed *H. armigera* of both sexes chose cotton-fed partners significantly more than peanut-fed individuals ones for mating when given a choice; however, peanut-fed males and females did not discriminate between the cotton- and peanut-fed partners. For experiments between cotton- and corn-fed larvae, there were no significant differences (table 3).

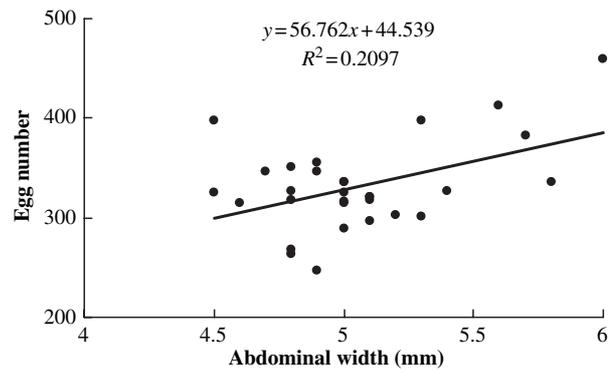


Fig. 1. Relationship between abdominal width and egg number ($r = 0.458$, $n = 30$, $P = 0.011$) in mated female *Helicoverpa armigera*

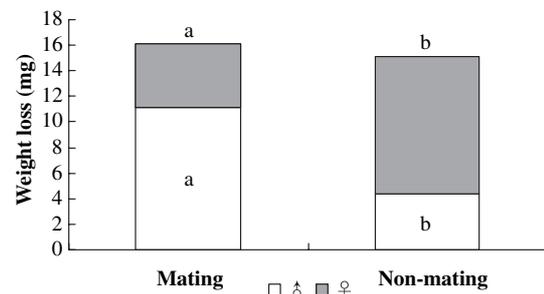


Fig. 2. Mean weight loss of mated and non-mated moths of *Helicoverpa armigera* in male and female selection experiment. Different letters indicate statistical significance at $P < 0.001$ (Student's *t*-test)

4 Discussion

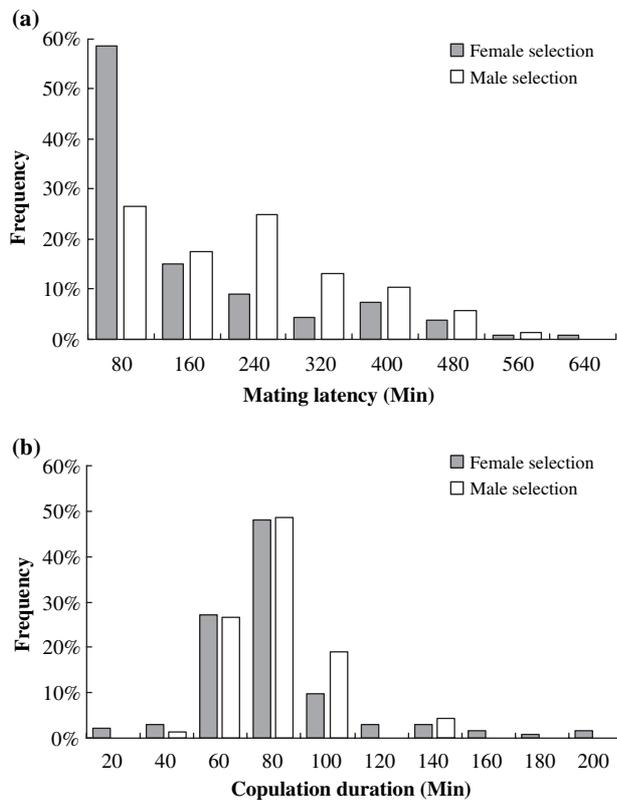
Although some moth species prefer mating partners with larger body size (VAN DONGEN et al., 1997; IYENGAR et al., 2002), this study demonstrated that *H. armigera* males and females neither preferred larger body size nor weight partners for mating. The result that body size having no effect on mating choice was similar to that of *Heliothis virescens* (KLEPETKA and GOULD, 1996). The abdominal width of selected female moths was significantly wider than that of non-selected moths, and there was a correlation between abdominal width

Table 1. Effect of body morphologic parameters and body mass on mate preference in *Helicoverpa armigera* moths

Characters	Selected (Mean ± SE)	Non-selected (Mean ± SE)	Statistical results			
Female characters in male selection	Length of body	15.45 ± 0.10 (mm)	15.40 ± 0.13 (mm)	$t = 0.365$	$P = 0.716$	Paired <i>t</i> -test, d.f. = 67
	Length of forewing	15.64 ± 0.08 (mm)	15.58 ± 0.11 (mm)	$t = 0.504$	$P = 0.616$	
	Body weight before mating	154.40 ± 2.53 (mg)	155.83 ± 3.23 (mg)	$t = -0.308$	$P = 0.759$	
	Body weight after mating	150.05 ± 2.07 (mg)	145.09 ± 2.81 (mg)	$t = 1.254$	$P = 0.214$	
	Abdominal width after mating	4.95 ± 0.04 (mm)	4.84 ± 0.05 (mm)	$t = 2.019$	$P = 0.048$	
	Weight loss	4.35 ± 1.31 (mg)	10.74 ± 1.19 (mg)	$F = 49.990$	$P < 0.001$	Student's <i>t</i> -test, d.f. = 135
Male characters in female selection	Length of body	16.34 ± 0.06 (mm)	16.46 ± 0.07 (mm)	$t = -1.415$	$P = 0.159$	Paired <i>t</i> -test, d.f. = 132
	Length of forewing	15.96 ± 0.06 (mm)	16.02 ± 0.07 (mm)	$t = -0.706$	$P = 0.482$	
	Body weight before mating	120.64 ± 1.41 (mg)	124.90 ± 1.37 (mg)	$t = 0.405$	$P = 0.686$	
	Body weight after mating	109.52 ± 1.37 (mg)	119.98 ± 1.36 (mg)	$t = -6.288$	$P < 0.001$	
	Weight loss	11.13 ± 0.33 (mg)	4.93 ± 0.13 (mg)	$F = 306.974$	$P < 0.001$	Student's <i>t</i> -test, d.f. = 265

Table 2. Mating latency and copulation duration of *Helicoverpa armigera* moths in male and female selection

	Male selection	Female selection
Mating latency between male and female selection	185.50 ± 15.58 (min)	110.94 ± 11.78 (min); $Z = -4.665$; $P < 0.001$; Wilcoxon–Mann–Whitney test, $n_{\text{male}} = 68$, $n_{\text{female}} = 133$
Copulation duration between male and female selection	70.84 ± 2.37 (min)	71.08 ± 2.54 (min); $Z = -0.631$; $P = 0.528$; Wilcoxon–Mann–Whitney test, $n_{\text{male}} = 68$, $n_{\text{female}} = 133$

**Fig. 3.** (a) Mating latency distribution for mate selection of female and male *Helicoverpa armigera* ($P < 0.0001$, $n_{\text{male}} = 68$, $n_{\text{female}} = 133$, Mann–Whitney test); (b) copulation duration distribution for mate selection of female and male *H. armigera* ($P = 0.528$, $n_{\text{male}} = 68$, $n_{\text{female}} = 133$, Mann–Whitney test)

and egg number. The result suggested the male moths would have an evolutionary benefit when they selected female moth with wider abdomen. The significant difference of weight loss between selected and non-selected male/female moths suggested that energy consumed by metabolism and moving resulted in weight loss and the transfer of spermatophore (mainly water) could improve the female body weight. The mating latency of male selection was significantly longer than that of female selection, which reflected that OSR positively affects the mating behaviour in *H. armigera*. There was no significant difference of copulation duration for both female and male selection, revealing that OSR processes no effect on copulation duration.

Helicoverpa armigera males seemed to be choosier than females when selecting partners for mating, contradicting Darwin's theoretical predictions that females should be more selective than males (SVENSSON,

Table 3. Effect of larval host plant experience on mating selection in *Helicoverpa armigera* moths and 1–3 for peanut, corn and cotton as host plant at larval stage, respectively (Binomial test)

Selectors	n	Partner		P
		Peanut	Cotton	
Peanut ¹				
Male	66	28	38	0.268
Female	60	27	33	0.519
Cotton ³				
Male	69	23	46	0.026
Female	64	17	47	<0.001
	n	Corn	Cotton	P
Corn ²				
Male	55	31	24	0.418
Female	61	28	33	0.525
Cotton ³				
Male	58	25	33	0.298
Female	64	29	33	0.703

1996). Male choosiness has also been reported for some *Lepidoptera* species (JIMÉNEZ-PÉREZ and WANG, 2004). The possible explanations of the evolution of choosier males in *H. armigera* may be a reflection of variation in characters. Females vary more in quality than do males, with the reproductive fitness of females highly depending on their age and virginity (LI et al., 1998; HOU and SHENG, 1999), but that of males varies less in morphological trait.

When served as selector, both female and male of cotton-fed moths preferred cotton- to peanut-fed for mate, but this preference did not occur for peanut moths. Several factors, alone or in combination, may be responsible for the results: (1) It is related with sex pheromone variation, and the non-selection of peanut adult may contribute to a wider broadness of the male selectivity spectrum. Sex pheromone variation mainly has three types: component structure, component ratio and component titer, and host deviation was considered to be one of the major reasons resulting in the pheromone variation (MCNEIL and DELISLE, 1989; LANDOLT and PHILLIPS, 1997; HUANG et al., 1998; PELOZUELO et al., 2004). At the experimental condition, sex pheromone variation likely came from the difference of host plant. Host plant difference at larval stage possesses potential effect on adult mate, for example the differentiation of pheromone production, which could act on mating success, and there are many reports suggesting that mating success can be diet-related (HENDRY et al., 1975; HENDRY, 1976; GUERIN et al., 1984; LÖFSTEDT et al., 1989; EMELIANOV et al., 2001; SHELLY et al., 2002). Variability in response of *H. armigera* males from different locations in India to

varying blends of female sex pheromone also suggests male sex pheromone response polymorphism (TAMHANKAR et al., 2003). (2) It is the effect of host on larval development, which consists of time different of pheromone release based on adult development, difference of patterns of female calling behaviour, effect of energy storage on mating behaviour, and so on. LIU et al. (2004) revealed that six plant species differ greatly in suitability as hosts for *H. armigera* when measure in terms of development, body weight, survivorship and reproduction, which could also affect mate behaviour. (3) The abdominal width of cotton-fed moths is wider than that of peanut-fed moth (unpublished data). But it can not explain that there was no preference of peanut-fed moth. It may be deduced that preference of a moth also depends on its own state, which needs further study.

The meaning for studying mate selection of *H. armigera* lays in the fact that non-random mating could, to certain extend, invalidate application of refuges for the use of transgenic *Bt* crops. The main crop served as refuge in north China is corn, which could be a vast refuge for third and fourth generation *H. armigera* but not for second generation *H. armigera*, so at that time the refuge function depends much on peanut, soya bean and other plants (WU et al., 2002). MALAUSA et al. (2005) found that European corn borer *Ostrinia nubilalis*, a target pest of *Bt*-toxins, showed assortative mating in sympatric host races. There are also reports about genetic differentiation of *H. armigera* larva and adults occurred between host groups in China (TAN et al., 2001; WANG et al., 2003). This result can provide a new way to explain the genetic differentiation between peanut and cotton host groups. It also indicates that corn, as an effective and ideal crop as refuge, is more efficient than peanut. Peanut along served as refuge crop may accelerate the evolution of resistant population, but in north China, the obvious overlap between the flight times of second- and early third-generation moths emerging from other host plants (WU et al., 2002) likely contributes to decrease the opportunity for assortative mating for moths *Bt* cotton and peanut. To improve the efficiency of refuge strategy, further research on mating selection according to field environment is also needed.

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References

- EMELIANOV, I.; DRE'S, M.; BALTENSWEILER, W.; MALLET, J., 2001: Host-induced assortative mating in host races of the larch budmoth. *Evolution* **55**, 2002–2010.
- EMLEN, S. T.; ORING, L. W., 1977: Ecology, sexual selection, and the evolution of mating systems. *Science* **197**, 215–223.
- Environmental Protection Agency, 1998: The Environmental Protection Agency's White Paper on *Bt* Plant-Pesticide Resistance Management. Washington: EPA Publication, 739-S-98-001.
- FITT, G. P., 1989: The ecology of *Heliothis* species in relation to agro-ecosystem. *Annu. Rev. Entomol.* **34**, 17–52.
- GOULD, F., 1998: Sustainability of transgenic insecticidal cultivars: integrating pest genetics and ecology. *Annu. Rev. Entomol.* **43**, 701–726.
- GUERIN, P. M.; BALTENSWEILER, W.; ARN, H.; BUSE, H. R., 1984: Host race pheromone polymorphism in the larch budmoth. *Experientia* **40**, 892–894.
- HALLIDAY, T. R., 1983: The study of mate choice. In: *Mate Choice*. Ed. by BATESON, P. Cambridge, United Kingdom: Cambridge University Press, 3–32.
- HENDRY, L. B., 1976: Insect pheromones: diet related? *Science* **192**, 143–145.
- HENDRY, L. B.; WICHMANN, J. K.; HINDENLANG, D. M.; MUMMA, R. O.; ANDERSON, M. E., 1975: Evidence for origin of insect sex pheromones: presence in food plants. *Science* **188**, 59–62.
- HOU, M. L.; SHENG, C. F., 1999: Fecundity and longevity of *Helicoverpa armigera* (Lepidoptera: Noctuidae): Effect of multiple mating. *J. Econ. Entomol.* **92**, 569–573.
- HOU, M. L.; SHENG, C. F., 2000: Calling behaviour of adult female *Helicoverpa armigera* (Hübner) (Lep., Noctuidae) of overwintering generation and effects of mating. *J. Appl. Entomol.* **124**, 71–75.
- HUANG, Y. P.; SHEN, J. H.; WANG, S. F.; TANG, D. W., 1998: Research progress in insect sex pheromone variation. *J. Cent. South Forestry Univ.* **18**, 88–95.
- IYENGAR, V. K.; REEVE, H. K.; EISNER, T., 2002: Paternal inheritance of a female moth's mating preference. *Nature* **419**, 830–832.
- JIMÉNEZ-PÉREZ, A.; WANG, Q., 2004: Sexual selection in *Cnephasia jactatana* (Lepidoptera: Tortricidae) in relation to age, virginity, and body size. *Ann. Entomol. Soc. Am.* **97**, 819–824.
- KIM, D. S.; LEE, J. H., 2002: Egg and larval survivorship of *Carposina sasakii* (Lepidoptera: Carposinidae) in apple and peach and their effects on adult population dynamics in orchards. *Environ. Entomol.* **31**, 686–692.
- KLEPETKA, B.; GOULD, F., 1996: Effects of age and size on mating in *Heliothis virescens* (Lepidoptera: Noctuidae): Implication for resistance management. *Environ. Entomol.* **25**, 993–1001.
- KOU, R.; CHOW, Y. S., 1987: Calling behavior of the cotton bollworm, *Heliothis armigera* (Lepidoptera: Noctuidae). *Ann. Entomol. Soc. of Am.* **80**, 490–493.
- LANDOLT, P. J.; PHILLIPS, T. W., 1997: Host plant influences on sex pheromone behavior of phytophagous insects. *Annu. Rev. Entomol.* **42**, 371–391.
- LI, G. Q.; CHEN, C. K.; HAN, Z. J.; WANG, Y. C., 1998: Sex maturity and mating habits of *Helicoverpa armigera* (Hübner). *J. Nanjing Agr. Univ.* **21**, 42–46.
- LIU, Z. D.; LI, D. M.; GONG, P. Y.; WU, K. J., 2004: Life table studies of the cotton bollworm, *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae), on different host plant. *Environ. Entomol.* **33**, 1570–1576.
- LÖFSTEDT, C.; VICKERS, N. J.; ROELOFS, W. L.; BAKER, T. C., 1989: Diet related courtship success in the oriental fruit moth, *Grapholitha molesta* (Tortricidae). *Oikos* **55**, 402–408.
- MALAUSA, T.; BETHENOD, M. T.; BONTEMPS, A.; BOURGUET, D.; CORNUET, J. M.; PONSARD, S., 2005: Assortative mating in sympatric host races of the European corn borer. *Science* **308**, 258–260.

- MCGAUGHEY, W. H.; WHALON, M. E., 1992: Managing insect resistance to *Bacillus thuringiensis* toxins. *Science* **258**, 1451–1455.
- McNEIL, J. N.; DELISLE, J., 1989: Are host plants important in pheromone-mediated mating systems of Lepidoptera? *Experientia* **45**, 236–240.
- PELOZUELO, L.; MALOSSE, C.; GENESTIER, G.; GUENEGO, H.; FREROT, B., 2004: Host-plant specialization in pheromone strains of the European corn borer *Ostrinia nubilalis* in France. *J. Chem. Ecol.* **30**, 335–352.
- SAS Institute Inc, 1988: SAS/STAT User's Guide, release 6.03 edn. SAS Institute, Car. SAS Institute Inc., North Carolina, USA.
- SHELLEY, T. E.; KENNELLY, S. S.; McINNIS, D. O., 2002: Effect of adult diet on signaling activity, mate attraction, and mating success in male Mediterranean fruit flies (Diptera: Tephritidae). *Florida Entomol.* **85**, 150–155.
- SVENSSON, M., 1996: Sex selection in moths: the role of chemical communication. *Biol. Rev.* **71**, 113–135.
- TAMHANKAR, A. J.; RAJENDRAN, T. P.; HARIPRASAD RAO, N.; LAVEKAR, R. C.; JEYAKUMAR, P.; MONGA, D.; BAMBAWALE, O. M., 2003: Variability in response of *Helicoverpa armigera* males from different locations in India to varying blends of female sex pheromone suggests male sex pheromone response polymorphism. *Curr. Sci.* **84**, 448–450.
- TAN, S. J.; CHEN, X. F.; LI, D. M.; ZHANG, H. Z., 2001: Can other host species of cotton bollworm be non-*Bt* refuges to prolong the effectiveness of *Bt*-cotton? *Chin. Sci. Bull.* **46**, 1804–1808.
- TSAI, J. H.; WANG, J. J., 2001: Effects of host plants on biology and life table parameters of *Aphid spiraecola* (Homoptera: Aphididae). *Environ. Entomol.* **30**, 45–50.
- VAN DONGEN, S.; MATTHYSEN, E.; SPRENGERS, E.; DHONDT, A. A., 1997: Mate selection by male winter moths *Operophtera Brumata* (Lepidoptera, Geometridae): adaptive male choice of female control? *Behaviour* **135**, 29–42.
- WANG, S. L.; XU, G.; YANG, X. W.; MA, J. S.; SHENG, C. F., 2003: Polymorphic studies on *Helicoverpa armigera* population in different host plants using microsatellite primers. *Cotton Sci.* **15**, 79–82.
- WU, K. J.; GONG, P. Y., 1997: A new and practical artificial diet for the cotton bollworm. *Entomol. Sin.* **4**, 227–282.
- WU, K. M.; GUO, Y. Y.; LV, N.; GREENPLATE, J. T.; DEATON, R., 2002: Evaluation of the natural refuge function for *Helicoverpa armigera* (Lepidoptera:Noctuidae) within *Bacillus thuringiensis* transgenic cotton growing areas in north China. *J. Econ. Entomol.* **95**, 832–837.
- ZALUCKI, M. P.; DAGLISH, G.; FIREMPONG, S.; TWINE, P., 1986: The biology and ecology of *Heliothis armigera* (Hübner) and *H. punctigera* Wallengren (Lepidoptera:Noctuidae) in Australia: what do we know? *Aust. J. Zool.* **34**, 779–814.

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