The influences of larval and adult food quality on the calling rate and pre-calling period of females of the cotton bollworm, *Helicoverpa armigera* Hübner (Lepidoptera: Noctuidae)

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**Abstract**

Pre-calling behavior of female adults of *Helicoverpa armigera* reared on artificial diet (Insecta LF) during the larval stage and fed on water and honey solutions (5, 10 and 20%) was observed. The quality of the adult diet did not influence the distribution of the pre-calling period (PCP). However, the calling rate was significantly higher in the three honey-fed groups (100%) than in the water-fed group (87.5%). In the next experiment, pre-calling behavior of female adults that were reared on Insecta LF during the larval stage and fed on 10% honey solution starting from different days after emergence was observed. The delay of adult feeding did not influence the calling rate, although the PCP was slightly prolonged in individuals which were not fed on honey solution until the onset of night 3 or night 5 (night 0=night of adult eclosion). In the experiment in which larvae were fed on different qualities of food (cotton leaf, okra fruit and Insecta LF), the calling rate varied greatly depending on the adult diet. When fed on honey solution, almost all adults called irrespective of their larval diet. However, when fed on water only, the calling rate of adults fed on Insecta LF during the larval period was 60.4%, while those of adults fed on cotton leaf and okra fruit were only 16.7% and 33.3%, respectively. These results indicate that most female adults of *H. armigera* can attain reproductive maturity even without feeding on nutritious diets when provided with highly nutritious diets during the larval period, and most female adults can not attain reproductive maturity without feeding on nutritious diets when provided with low nutritive value diets during the larval period.

**Key words:** *Helicoverpa armigera*, larval diet, adult diet, pre-calling period, reproductive maturity

**INTRODUCTION**

The cotton bollworm, *Helicoverpa armigera* Hübner, is a major agricultural pest distributed in many parts of the world (Pearson, 1958; Fitt, 1989). Its larvae attack a wide range of cultivated and wild host plants. In Japan, its population densities had been generally low until outbreaks occurred in some areas of western Japan in 1994 (Yoshimatsu, 1994).

*H. armigera* is capable of long-distance migratory flights (Coombs et al., 1993; Gregg, 1993; Gregg et al., 1993). Such movements are believed to be undertaken by reproductively immature adults (Coombs et al., 1993; Colvin and Gatehouse, 1993a, c; Armes and Cooter, 1991) in response to a general deterioration of the current habitat (Fitt, 1989; Riley et al., 1992). Fitt (1989) suggested that a habitat deteriorates when there is a shortage of nectar sources or larval hosts, a condition which can not ensure the survival of the adults and successful establishment of their offspring.

Larval and adult nutrition may play crucial roles in the attainment of reproductive maturity in the noctuid moths, including *H. armigera*. Colvin and Gatehouse (1993a) have found that moths of both sexes of *H. armigera* took significantly longer to reach reproductive maturity when fed on water from night 0 (night of eclosion) to night 4 followed by sugar solution thereafter, than those given sugar solution from night 0. Adult feeding has been considered to be a requirement for mating and egg laying in *H. armigera* (Hardwick, 1965) and in *Heliothis zea* (Callahan, 1962). However, both mating and oviposition were also observed in unfed *H. zea* and *H. virescens* females formed from larvae fed on nutritious diets (Lukefahr and Martin, 1964), suggesting that the nature of the larval and adult food quality influences the calling rate and pre-calling period of female adults of *H. armigera*.
diets influences the attainment of reproductive maturity in these species.

This study aimed to determine the influences of adult food quality, adult feeding regime and the combination of larval and adult diets on the pre-calling period (PCP) of females in H. armigera populations collected from western Japan.

MATERIALS AND METHODS

Experimental conditions. The experiment was conducted in a small room (1.70 m in length \times 1.70 m in width \times 1.98 m in height). Photoregime was 16L8D and temperature was 25\pm 1^\circ C. Light during the day was provided by five 20-watt fluorescent lamps while background illumination at night was provided by a 60-watt bulb placed inside a black plastic container with several small holes on top.

Test insects. The three populations used in the experiments were all collected from nearly the same site in Ushimado, Okayama Prefecture. The F\textsubscript{1} laboratory generation offspring of the population collected on cabbage in September, 1996 was used for the study on adult diet. The F\textsubscript{1} offspring of the population collected on cherry tomato in November, 1997, was used for the study on adult feeding regime. The F\textsubscript{1} offspring of the population collected on cabbage in October, 1998, was used for the study on larval and adult food combinations.

General rearing procedure. Late-stadia larvae collected from the field were individually reared in 50-ml glass vials and fed on slices of Insecta LF (Nihon-Nosan-Kogyo Co.). In order to facilitate aeration, a small hole (1.5 mm in diameter) was drilled into the center of the vial cap. Larval food was replenished every 4 days. When the insects reached the pre-pupal stage, they bored into the remaining diet and pupated. One-week-old pupae were transferred into plastic trays half-filled with small kitchen paper towelling.

Upon adult emergence, 8 to 10 pairs of females and males were transferred into each screen cage (30 cm \times 30 cm \times 30 cm) wherein they mated freely. They were fed on 10\% (w/v) honey solution in Petri dishes lined with thin cotton sheetings and covered with parafilm having several holes made using a paper hole puncher. Two to three thin cotton sheetings were taped on the side walls of each cage and served as the substrate for oviposition. The egg-containing sheets were harvested daily and subsequently replaced with new ones. By using a small scissors, these egg-containing substrates were cut into small strips, put into Petri dishes and covered.

The effect of adult food on the PCP. Successive rearing in the laboratory followed the general rearing procedure. First-stadium larvae were reared in mass on Insecta LF in Petri dishes. In order to avoid cannibalism, individual rearing of larvae in 50-ml glass vials was started from the 3rd-stadium. The pre-pupae bored and pupated into the diet. One-week-old pupae were harvested and sorted according to sex on the basis of the genital and anal configurations. Female pupae were confined separately in plastic trays half-filled with small paper towelling and covered. When the female pupae turned blackish (sign of imminent eclosion), they were individually put into the 900-ml plastic containers with several 2-mm holes on two sides and on the cover. A cotton was saturated with the desired honey concentration was put into the cap of a 50-ml glass vial which was placed inside the 900-ml plastic container as adult food. The following were the different adult diets used in this study: 1) distilled water, 2) 5\% honey solution, 3) 10\% honey solution, and 4) 20\% honey solution. The honey solutions were prepared on a weight/volume basis. The diets were provided to the adults starting from night 0 until they called, and, were renewed daily.

The effect of adult feeding regime on the PCP. There were 5 treatments in this study, 1) adults fed on 10\% honey solution from night 0 until they called, 2) adults fed on distilled water on night 0 and 10\% honey solution from night 1 until they called, 3) adults fed on water from night 0 until night 2 and 10\% honey solution from night 3 until they called, 4) adults fed on water from night 0 until night 4 and 10\% honey solution from night 5 until they called, and 5) adults fed on distilled water from night 0 until they called or died. The honey solutions were provided to the moths about 2-4 h prior to the onset of the nights specified in the treatments and renewed daily until they called or died.

The effect of larval and adult diet combinations on PCP. Young cotton leaf, young okra fruit and Insecta LF were used as larval food in this
study. The cotton leaves were taken from cotton plants established in two small fields inside the Okayama University campus in late spring and early summer 1998, while the okra fruits were bought from commercial establishments. Around 10 young cotton leaves were placed into each 900-ml plastic container wherein around 100 1st-stadium larvae were reared in mass. The larvae were transferred into new containers with fresh cotton leaves daily until they reached the 2nd-stadium. From the 3rd-stadium they were individually reared in 50-ml glass vials. Those reared on okra fruit and Insecta LF were likewise fed in mass in a 900-ml plastic container until the 2nd-stadium and individually reared in 50-ml glass vials starting from the 3rd-stadium. The female pupae formed from each larval diet were divided into 2 groups. Female adults which emerged from one group were fed on 10% honey solution and those from the other group were fed solely on distilled water starting on night 0 until they either called or died.

PCP assessment. The PCP of a female was determined following the method of Colvin and Gatehouse (1993a, b) wherein the night of moth eclosion was designated as night 0 and the period until the night at which a female started to call was designated as her PCP. A calling female can be recognized by the extruded ovipositor (Kou and Chow, 1987). In our previous study (Casimero et al., 1999), we observed that calling by females of two H. armigera populations collected from two locations in Okayama Prefecture occurred in the 2nd half of the night, so in the present study we observed the calling behavior in this period. A penlight with red illumination whose brightness was reduced to a level just bright enough to see the extruded ovipositor of the female was used to observe the calling behavior.

RESULTS

The effect of adult diet on the PCP

The different honey solutions (5, 10, 20%) and distilled water (control treatment) did not influence the mean PCP of the females (p>0.05, Scheffé's F-test) that called before they died (Fig. 1). In this figure, the percentages of females which called on particular nights were calculated based on the total number of samples in each treatment, while the mean PCP values were derived from the females which called (this calculation procedure was also used for the PCP data in the other two experiments). Irrespective of the quality of the adult diet, more or less 30% of the sample adults called for the first time on night 1 and the largest proportion (40.0–45.2%) called on night 2. The remaining honey-fed adults called on nights 3 and 4 while the rest of the water-fed individuals called on night 3 but none called on night 4. Although the mean PCP of the females fed solely on water did not vary significantly from that in those fed on honey at different concentrations, a significant proportion of the water-fed group (12.5%) failed to call and thus remained reproductively immature until their death (Table 1). All females fed on honey at any given concentration called before they died.

![Fig. 1. Pre-calling period distributions and means (±SD) of H. armigera females fed on different adult diets.](image)

<table>
<thead>
<tr>
<th>Adult diet</th>
<th>n</th>
<th>% of females that called</th>
</tr>
</thead>
<tbody>
<tr>
<td>Water (control)</td>
<td>32</td>
<td>87.5</td>
</tr>
<tr>
<td>5% honey solution</td>
<td>39</td>
<td>100.0*</td>
</tr>
<tr>
<td>10% honey solution</td>
<td>42</td>
<td>100.0*</td>
</tr>
<tr>
<td>20% honey solution</td>
<td>40</td>
<td>100.0*</td>
</tr>
</tbody>
</table>

* * Significant difference at p<0.05 between the honey solutions and control treatment (Fisher's exact probability test).
The effect of adult feeding regime on the PCP

Delayed feeding of honey (10% w/v) to the female moths until night 5 only slightly prolonged the mean PCP ($p > 0.05$, Scheffe's $F$-test) (Fig. 2). A markedly shorter PCP was observed in those fed on water but this value was derived only from those which called (76.2%). Further, for the water-fed group, the latest females to call for the first time were recorded on night 4. On the other hand, the late-calling females in the other treatments were observed until the 6th night. Around 76.0% of the water-fed females called and this proportion was significantly lower than that for females fed on honey on night 0 as well as in those fed on honey solution in delayed schedules wherein only one individual failed to call (Table 2).

The effect of larval and adult food combinations on the PCP

The influences of the larval and adult food combinations on female PCP are presented in Fig. 3. The differences in the mean PCP values among the treatments were insignificant ($p > 0.05$, Scheffe's $F$-test). However, it may not be ideal to compare the PCP of water-fed adults to that of honey-fed ones because only a small percentage of the former group, called especially among those fed on cotton leaf (16.7%) and okra fruit (33.3%) during the larval stage. When the PCP values of the honey-fed adults in all larval groups were compared, the differences in the mean values were insignificant. However, a greater proportion of honey-fed adults in the group fed on cotton leaf called on night 1 but a smaller proportion called on night 2 when compared with the other groups. Irrespective of larval diet, calling (first time) by honey-fed adults ranged from night 1 to night 7. While the commencement of calling by females fed on water in all groups was observed on night 1, none called beyond night

Table 2. Percentage calling by *H. armigera* females as influenced by the different adult feeding regimes

<table>
<thead>
<tr>
<th>Adult feeding regime</th>
<th>$n$</th>
<th>% of females that called</th>
</tr>
</thead>
<tbody>
<tr>
<td>10% honey solution fed on night 0</td>
<td>41</td>
<td>97.6**b</td>
</tr>
<tr>
<td>10% honey solution fed on night 1</td>
<td>46</td>
<td>100.0***</td>
</tr>
<tr>
<td>10% honey solution fed on night 3</td>
<td>44</td>
<td>100.0***</td>
</tr>
<tr>
<td>10% honey solution fed on night 5</td>
<td>38</td>
<td>100.0***</td>
</tr>
<tr>
<td>Water fed from night 0 until females called or died (control)</td>
<td>42</td>
<td>76.2</td>
</tr>
</tbody>
</table>

*For the treatments that involved delayed feeding of 10% honey solution (nights 1, 3 and 5), distilled water was provided to the moths on the previous nights.

** Significant difference at $p < 0.01$, 0.001, respectively, between adult feeding regimes and control treatment (Fisher's exact probability test).
The Influences of Larval and Adult Food

The proportion of females that called was significantly greater in those fed on 10% honey solution than in those fed on water. With the exception of one female, all those fed on 10% honey solution had called before they died. In contrast, only 16.7% of the water-fed females which had emerged from the larvae fed on cotton leaf called, while 33.3% and 60.4% of the water-fed adults which had emerged from larvae fed on okra fruit and Insecta LF, respectively, called.

DISCUSSION

The cotton bollworm, Helicoverpa armigera, is considered to be a facultative migrant which undertakes long-distance flights in response to deterioration in the current habitat (Fitt, 1989; Riley et al., 1992). Colvin (1995) suggested that nectar from flowering plants may serve as an important environmental cue that signals both the present suitability of the habitat for adult reproduction and its future suitability for larval development. This argument is strongly supported by common observations that for the majority of moths in this species, carbohydrate is required for reproductive maturation (Hardwick, 1965; Colvin and Gatehouse, 1993a) and female moths tended to prefer laying their eggs near the flowers or reproductive parts of host plants (Roome, 1975; Wardaugh et al., 1980; Alvarado-Rodriguez et al., 1982; Firempong and Zalucki, 1990).

The results of the present study on adult diet quality show that the calling rate (percentage of females that called) of H. armigera female adults formed from larvae fed on the artificial diet Insecta LF was not significantly influenced by the different honey solutions (5, 10 and 20%). In addition, the mean PCP values of the females fed on distilled water throughout their lives were comparable to the PCP of the ones fed on these honey solutions. However, about 13% of the water-fed females died without calling. The results imply that the majority of females can reach reproductive maturity even when given only a diet of water. Further, a low concentration of honey solution (5%) enhanced the sexual maturation of adults in a similar manner to the more concentrated diets. In an adult feeding experiment involving the oriental armyworm, Pseudaletia separata, Kanda (1987) found that females absorbed significantly greater amounts of

2 and night 4 in those fed on cotton leaf and okra fruit, respectively. On the other hand, calling was observed until night 6 in those fed on Insecta LF. This clearly resulted in smaller mean PCP values for those fed on cotton leaf and okra fruit compared to those fed on Insecta LF.

Table 3 compares the proportion of females that called before their death as influenced by larval and adult food combinations. For each of the

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<td></td>
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***Significant difference at p < 0.001 between the honey- and water-fed adults in each larval diet group (Fisher's exact probability test).

Fig. 3. Influence of larval and adult diet combinations on the pre-calling period distributions and means (± SD) of H. armigera females.

Table 3. Percentage calling by honey- and water-fed H. armigera females that emerged from larvae fed on different diets.

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solutions when fed on 1%, 3% and 5% sucrose solutions compared to those fed on 10% and 30% sucrose solutions, but the total amount of sucrose absorbed per female increased with increasing concentrations of the sucrose solution. In the present experiment, we did not measure the amount of honey solutions absorbed by the females. However, assuming that food absorption by females in *H. armigera* was similar to that observed in *P. separata*, it appears that 5% honey solution is sufficient to support reproductive maturation of females in *H. armigera*.

Although a considerable proportion (23.8%) of females fed solely on water throughout their lives died without calling (Table 2), delayed feeding of 10% honey solution to the female adults until prior to night 5 only slightly prolonged the PCP (Fig. 2). This was contrary to the results of Colvin and Gatehouse (1993a) who found that the majority of moths failed to call when fed on water only from night 0 to night 4, but did so when sugar solution was fed to them thereafter. The conflicting results were perhaps due to the nature of the larval diets used. In their experiment, a diet of fresh sorghum or sunflower seed was fed to the larvae, whereas in our experiment the artificial diet Insecta LF was used. One common observation in both studies, however, was that the moths that seemed unable to call when fed only on water tended to call when a diet of honey was provided. The results of our previous study on larval survival and development of *H. armigera* revealed that the weight of the pupae formed from the larvae fed on Insecta LF was significantly heavier than in those fed on a number of host plants including okra fruit and cotton leaf (Casimero et al., 2000). The moths which emerged from the larvae fed on Insecta LF might have accumulated sufficient energy reserves to achieve reproductive maturation even without access to sugar.

In other noctuids, both mating and oviposition has been recorded in fed and unfed female adults. Lukefahr and Martin (1964) observed that unfed adult *H. zea* and *H. virescens* that emerged from larvae fed on artificial diet and corn mated and oviposited, while those that emerged from larvae fed on cotton squares failed to do so unless provided with a sucrose solution. In *P. separata*, the starvation period of females ranging from 1 to 5 days only slightly delayed their previposition period (Kanda, 1987).

The results of our experiment on larval and adult food combinations show that larval food had no significant effect on the calling rate when 10% honey solution was provided to the adults starting from night 0 and renewed daily thereafter until they called. However, variation in the distributions of the PCP and the calling rate was evident when the female moths were fed solely on water. No water-fed females called for the first time later than nights 2 and 4 in those reared on cotton leaf and okra fruit, respectively (Fig. 3). On the other hand, calling was observed until night 6 in the water-fed moths provided with Insecta LF during the larval stage (Fig. 3). Further, the percentage of water-fed females which called was substantially greater in those fed on Insecta LF (60.4%) compared to those reared on okra fruit (33.3%) and cotton leaf (16.7%) (Table 3). Topper (1987a) observed that water-fed *H. armigera* females reared on groundnuts and sorghum during the larval stage had average lifespans of 2.8 and 3.5 days, respectively, implying that it was unlikely for both groups to have reached reproductive maturity. He observed however, that the average lifespan in sugar-fed females reared on groundnuts and sorghum was prolonged 2.5 and 2.1 fold, respectively. Lukefahr and Martin (1964) reported that sugar-fed females of *H. zea* reared on an artificial medium, corn and cotton squares in the larval stage produced comparable proportions of fertile individuals. They also found that the majority of individuals reared on artificial medium, corn and cotton boll were fertile even when given only a diet of water in the adult stage, whereas those reared on cotton square provided a diet of water were all infertile. A nutritious adult food seemed to have effectively offset the unfavorable effects brought about by poor larval diet. These results indicate that larval and adult food had a combined influence on the attainment of reproductive maturity in *H. armigera* females.

In our present experiments, although different *H. armigera* populations were used, some of the water-fed female adults failed to call even when given a larval diet of Insecta LF, and the percentage of such adults tended to increase in populations with longer PCPs. Possibly, the individuals with longer PCPs were more likely to have failed in reaching reproductive maturity.

It is widely believed that *H. armigera* adults mi-
grate in response to a shortage in the source of adult and larval diets. Using plant pollen as markers for migrating *H. armigera* and *H. punctigera*, Gregg (1993), however, found that moths captured in eastern Australia contained pollen of flowering plants found in western Australia and in between these sites, suggesting that they had fed on plant nectar before migration occurred and possibly at stopovers on the way. For the majority of *H. armigera* moths, it has been observed that reproductive maturation was rather fast when fed on a diet of sugar solution (Colvin and Gatehouse, 1993a; Coombs, 1997). In our present studies, the majority of honey-fed adults called on night 3. These observations suggest that the time available for migration in this species is very short for a majority of moths if long-distance flights are exclusively undertaken by reproductively immature adults as commonly observed (Armes and Cooter, 1991; Colvin and Gatehouse, 1993b; Coombs et al., 1993).

Topper (1987a) found that flight activity of the majority of males, inseminated females and virgin females of *H. armigera* peaked at dusk and greater proportions of them were active at sites where adult food was scarce (i.e. pre-flowering cotton) compared to at sites where honeydew and nectar were plentiful (i.e. tassel-stage sorghum). He also observed that flight activity at sites with bountiful adult food started to decline somewhat earlier and more quickly. The 2nd peak of male activity observed in the 2nd half of the night was probably associated with mate-finding flights. He also noted that moth densities in fields where adult food was plentiful were 20 times more than that in fields where adult food was scarce, suggesting that *H. armigera* moths are sedentary in areas where flowering plants are present. The moths were attracted to sorghum at the tassel stage mainly for feeding and egg deposition (Topper, 1987b). However, it was not known whether emigration was the causal factor behind the much smaller number of moths recorded in areas with scarce adult food.

The achievement of reproductive maturity in some of the water-fed moths which emerged from the *Insecta* LF-fed larvae and most of the okra fruit- and cotton leaf-fed larvae appeared to have been delayed indefinitely as they failed to call during their adult life (Tables 1–3). But this may not necessarily indicate a corresponding indefinite ex- tension in the period at which long-distance migration occurs. In a tethered-flight experiment, Coombs (1997) discovered that in early adult life the flight capabilities of water- and sugar-fed *H. armigera* were comparable but starting on night 4 (peak flights were recorded) there was a substantial reduction in the flight performance of adults given a diet of water only.

Our present experiments suggested that larval and adult nutrition had a combined marked influence on the attainment of reproductive maturity of *H. armigera* females. Determination of whether such influence of diets on the PCP has a positive implication to the flight ability of *H. armigera* may be an important topic for future research.

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