

# Effects of Survival Rate and Fecundity on the Intrinsic Rate of Increase of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae)

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## ABSTRACT

The life history data of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) kept at 25°C on an artificial diet, on hybrid sweet corn, and on asparagus, as well as those kept at 29°C on an artificial diet were analyzed to assess the effects of survival rate and fecundity on the intrinsic rate of increase ( $r$ ). The curtailed intrinsic rate ( $r_{\delta}$ ) describes the effects of survivorship and fecundity on the intrinsic rate of increase. The curtailed intrinsic rate of *H. armigera* was estimated by applying the age-stage, two-sex life table theory, and ranged from negative to positive and finally became equal to the intrinsic rate. The cumulative contribution ( $r_y$ ) is a descriptive value of the cumulative input of individuals surviving to age  $y$  to the intrinsic rate. The value of cumulative contribution ( $r_y$ ) ranges from zero to  $r$ , however, it is not an intrinsic rate. At the beginning of a life table study of *H. armigera* using a fixed hatch rate, a cohort consists of unfertile eggs, and calculating the fecundity from the total laid-eggs by ignoring their hatchability does not reflect the true biological characteristics of *H. armigera*. Rather, it shifts the survivorship curve downward, the fecundity curve upward, and provides very high estimates of the life table parameters. In addition, it reduces the reliability of the estimate of the intrinsic rate of increase to be used as an indicator to evaluate the performance and fitness of *H. armigera* under variable conditions. Therefore, we recommend that the fecundity be calculated using the number of viable eggs. In addition, the age-stage, two-sex life table should be used in order to accurately analyze the data to encompass the age-specific variation in sex ratio, hatchability, and development in the analysis.

**Key words:** *Helicoverpa armigera*, sex ratio, hatchability, curtailed intrinsic rate

## Introduction

*Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) is a pest with a high economic impact on agriculture worldwide. This insect achieves its pest status by being polyphagous, highly mobile, highly fecund, and because it undergoes facultative diapause (Fitt, 1989). These characteristics enable this pest to survive in various habitats and adapt to seasonal changes. It has a wide host range (Zalucki *et al.*, 1986; Zalucki *et al.*, 1994; Liu *et al.*, 2004) including corn (*Zea mays* L.), tomato (*Solanumly copersicum* L.), asparagus (*Asparagus officinalis* L.), and cotton (*Gossypium* spp.). The hatchability of eggs varies with the maternal age (Jha *et al.*, 2012a; b). When in the larval stage it undergoes 5-7 molts depending on food and environmental condition (Fitt, 1989; Casimero *et al.*, 2000). The growth, development, and consumption rate varies among individuals in a cohort. Sex differentiation can only be done in the pupal stage. A cohort of *H. armigera* consists of two sexes-male and female varying in offspring sex ratio depending on the age of the cohort (Jha *et al.*, 2012a; b). These are some of the observable biological variations that affect the demography of this insect and complicates our ability to evaluate its fitness and damage potentiality under varying conditions. Life table parameters are important measures that can be used for monitoring the fitness of this insect (Iranipour *et al.*, 2010).

The two categories of life table parameters that can be obtained from a life table study are: the basic parameters and derived parameters (Farhadi *et al.*, 2011; Huang and Chi, 2012). The survival rate and fecundity are the basic parameters that are calculated directly from the life history data of a cohort. These basic parameters are used to estimate the derived parameters such as the intrinsic rate of increase ( $r$ ), finite rate of increase

( $\lambda$ ), mean generation time ( $T$ ), and the net reproductive rate ( $R_0$ ). Thus, survivorship and fecundity are components of the derived parameters, and the derived parameters reflect the combined effects of these basic parameters.

In general, survival and reproductive success are used to measure the fitness of an insect under a certain ecological condition. As a fitness indicator, they are used either separately (Naseri *et al.*, 2010) or in combination (Caprioa *et al.*, 2009). Development time is another key feature that affects fitness (Kingsolver and Huey, 2008). In addition to the aforementioned indicators, several other fitness indicators including body size and weight (Liu *et al.*, 2004), and the nutritional indices of immatures (Ahmad, 2002; Naseri *et al.*, 2010), are used in the ecological study of insects. Thus, the appropriateness of a fitness indicator is determined by the ecological context and objectives (Roff, 2002). However, the intrinsic rate of increase ( $r$ ) is considered to be the most appropriate and comprehensive parameter for evaluating the ecological fitness of an insect under varying conditions (Southwood, 1966; Smith, 1991). The intrinsic rate of increase is the per capita rate of population increase in a closed population with a stable age distribution, and is derived from age-specific schedules of survival and reproduction. It is more appropriate in cases where there is a substantial variation in survivorship, fecundity, and generation time among individuals of a population. This case typically occurs in species like *H. armigera* which reproduce continuously, or have many generations in a year (Kingsolver and Huey, 2008).

A laboratory life table is key for estimating the intrinsic rate of increase under a given set of conditions (Gutierrez, 1996). In this study, the age-stage, two-sex life table approach (Chi and Liu, 1985; Chi, 1988) was used to estimate the curtailed intrinsic rate of increase based on laboratory life tables. The curtailed

intrinsic rate of increase was calculated to describe the effects of survival rate and fecundity on the intrinsic rate of increase (Chi and Su, 2006). We concluded that the age-stage, two-sex life table offers a precise and comprehensive means for assessing the effects of survivorship and fecundity on the evaluation of the ecological fitness of insects and mites.

## Materials and Methods

### Life History Data

The rearing method and life table study at 25°C on an artificial diet, and on hybrid sweet corn, as well as at 29°C on an artificial diet are well described in Jha *et al.* (2012a) and Jha *et al.* (2012b). Similar procedures were followed for the rearing and life table study on asparagus. Asparagus (*Asparagus officinalis*) foliage was obtained from pesticide free plants grown in a farmer's field in Caotun, Nantou County, Taiwan. A batch of healthy young asparagus foliage was brought from the field every 2-3 days during the experiment. The lateral branches were excised, and the stems of the excised branches were placed into water to protect the foliage from drying out. The foliage was provided to the *H. armigera* as food.

In total, 110 hatched eggs were used to begin the life table of *H. armigera* rearing on asparagus. The newly hatched larvae were individually transferred to Petri dishes (9 cm diameter) using a fine brush and were then reared as a group up to second instar. The third and older instars were reared individually in Petri dishes (9 cm diameter) on asparagus foliage. The individual larvae were observed daily for molting and survivorship. The asparagus foliage was replaced daily. The larva that entered into the prepupal stage were provided with decomposed peat-based compost (Blocking Compost by Plantflor Humus Verkaufs GmbH, D 49377 Vechta, Germany) for pupation. Each pupa was sexed, weighed, and then kept in an

individual plastic cup (9 cm diameter by 5.5 cm high). Newly emerged adults were paired in oviposition containers lined with paper towel and transferred to a new container on a daily basis. Eggs laid by each female at different ages were collected and kept separately to record the hatch rates. If a moth died earlier than its mate, it would be replaced by a new one from the mass rearing colony. The data from these replacement recruits were excluded from the analysis.

### Demographic analysis

The raw data was analyzed based on the theory of the age-stage, two-sex life table (Chi and Liu, 1985; Chi, 1988). The age-specific survival rate ( $l_x$ ) and the age-specific fecundity ( $m_x$ ) were calculated from the daily records of survival and fecundity of all individuals in the cohort. The age-specific survival rate ( $l_x$ ) is the probability that a newborn survives to age  $x$  and was calculated as  $l_x = \sum_{j=1}^m s_{xj}$  where  $m$  is the number of stages and  $s_{xj}$  is the age-stage specific survival rate. In other words,  $s_{xj}$  is the survivorship of a newborn to age  $x$  and stage  $j$ . The age-specific fecundity ( $m_x$ ) was calculated as  $m_x = \left( \sum_{j=1}^m s_{xj} f_{xj} \right) / \sum_{j=1}^m s_{xj}$ . The age-stage specific fecundity ( $f_{xj}$ ) is the number of eggs produced by every individual of age  $x$  and stage  $j$ . In this study,  $f_{xj}$  was calculated from the number of hatched eggs since that reflects the true biological characteristics of *H. armigera*. In addition, any unhatched eggs were excluded from the parent cohort in the beginning of the study. The mean female fecundity ( $F$ ) was calculated as  $F = \sum_{i=1}^{n_0} B_i / n_0$  where  $n_0$  is the total number of females in the cohort and  $B_i$  is the total fecundity of individual  $i$ .

The intrinsic rate of increase ( $r$ ) was estimated using the iterative bisection method from the Euler-Lotka formula (Eq. 1) with the age indexed from 0 (Goodman, 1982):

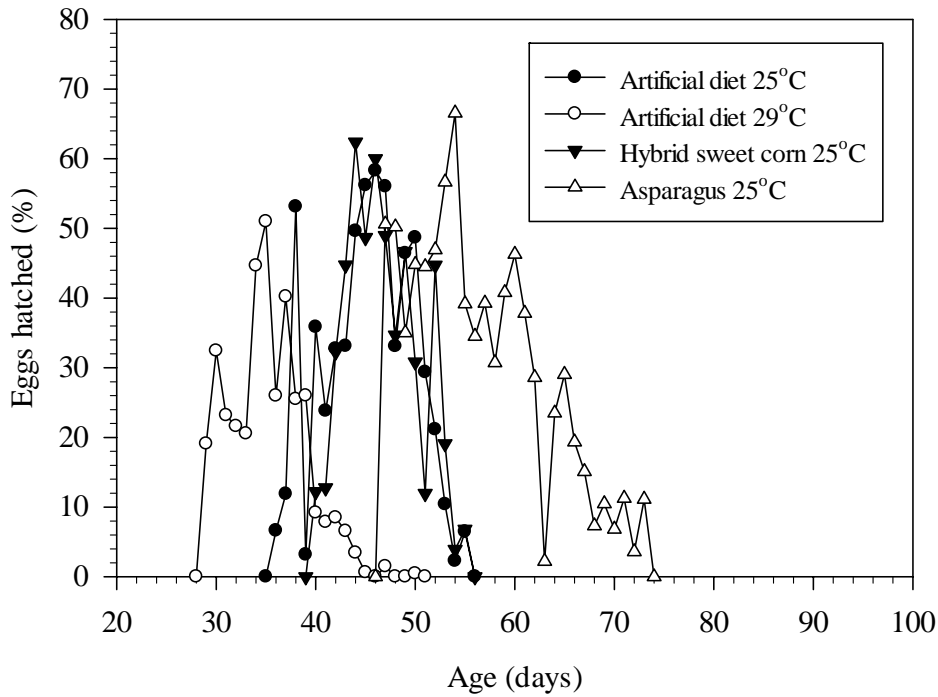


Fig. 1. The age-specific egg hatch rates of *Helicoverpa armiger* (The data of Jha *et al.* 2012 a; b were analyzed and included for comparison.)

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1 \quad (1)$$

The bisection method can be found in most textbooks on numerical analysis (Burden and Faires, 2005). The curtailed intrinsic rate of increase ( $r_{\delta}$ ) was estimated as (Chi and Su, 2006)

$$\sum_{x=0}^{\delta} e^{-r_{\delta}(x+1)} l_x m_x = 1 \quad (2)$$

where  $\delta$  is the discard age. In this case, the intrinsic rate of increase ( $r_{\delta}$ ) of the population was estimated by assuming that it survived only to age  $\delta$ , and that the  $l_x$  and  $m_x$  beyond  $\delta$  were discarded. The cumulative contribution ( $r_y$ ) of age  $y$  to the intrinsic rate was calculated as (Chi and Su, 2006)

$$r_y = r \cdot \sum_{x=0}^y e^{-r(x+1)} l_x m_x = 1 \quad (3)$$

The value of  $r$  estimated using Eq. 1 was used in Eq. 3 to calculate  $r_y$ . The analysis was performed using the computer program TWSEX-MSChart (Chi, 2012), designed in Visual BASIC (Version 6.0 Service pack 6) for Windows. This program is available at <http://140.120.197.173/Ecology/prod02.htm> (National Chung Hsing University, Taichung, Taiwan) and <http://nhsgbig.inhs.uiuc.edu/wes/chi.html> (Illinois Natural History Survey).

## Result

The age-specific hatchability of eggs and the variation in the sex ratio of the offspring with cohort age of *H. armigera* reared at 25°C on an artificial diet, hybrid sweet corn, and asparagus and at 29°C on artificial diet are plotted in Figs. 1 and 2

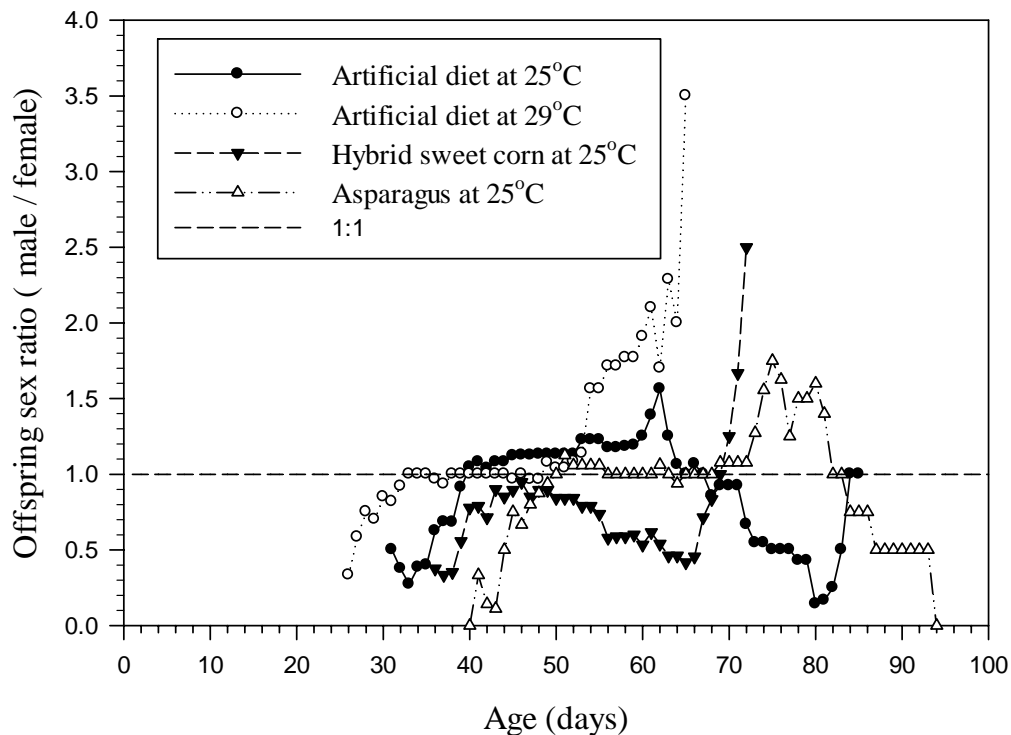


Fig. 2. The age-specific offspring sex ratio of *Helicoverpa armigera*. (The data of Jha *et al.* 2012a; b were analyzed and included for comparison.)

respectively. The curve of  $r_{\delta}$  using total eggs is plotted in Fig. 3, and precedes the curve of  $r_{\delta}$  using hatched eggs. The value of  $r_{\delta}$  ranges from negative to positive value. The negative values of  $r_{\delta}$  were obtained from the life table data of *H. armigera* reared at 25°C on an artificial diet, and on hybrid sweet corn, and at 29°C on an artificial diet. However, the negative value of  $r_{\delta}$  did not prevail in the case of rearing *H. armigera* on asparagus at 25°C. The negative value of  $r_{\delta}$  indicates that the population will decrease if a cohort survives only to this age. For the analysis, the estimated values of  $r_{\delta}$  were classified into three distinct categories, a negative value ( $r_{\delta} < 0$ ), a positive value ( $r_{\delta} > 0$ ), and a maximum value ( $r_{\delta} = r$ ). The age ( $y$ ) corresponding to the start of these categories is given in Table 1.

The age ( $y$ ) at  $V_{\delta-ve}$  is the day at which the reproduction begins and the value of  $r_{\delta} < 0$  occurs for the first time. This is the minimum duration that the cohort has to survive after the beginning of reproduction. The age ( $y$ ) at  $V_{\delta+ve}$  is the first day at which the positive value of  $r_{\delta}$  is estimated, i.e.,  $r_{\delta} > 0$ . If the cohort survives to an age where  $r_{\delta}$  becomes greater than zero, then the population begins to increase. The age ( $y$ ) at  $V_{\delta_{max}}$  is the day at which the curtailed intrinsic rate becomes equal to the intrinsic rate of increase of the cohort ( $r$ ) and  $y_{last}$  is the last age of the cohort. The post-reproductive duration is the time period during which the survivors do not make any contribution to  $r$ . It is expressed in a percentage of cohort longevity, and is calculated as

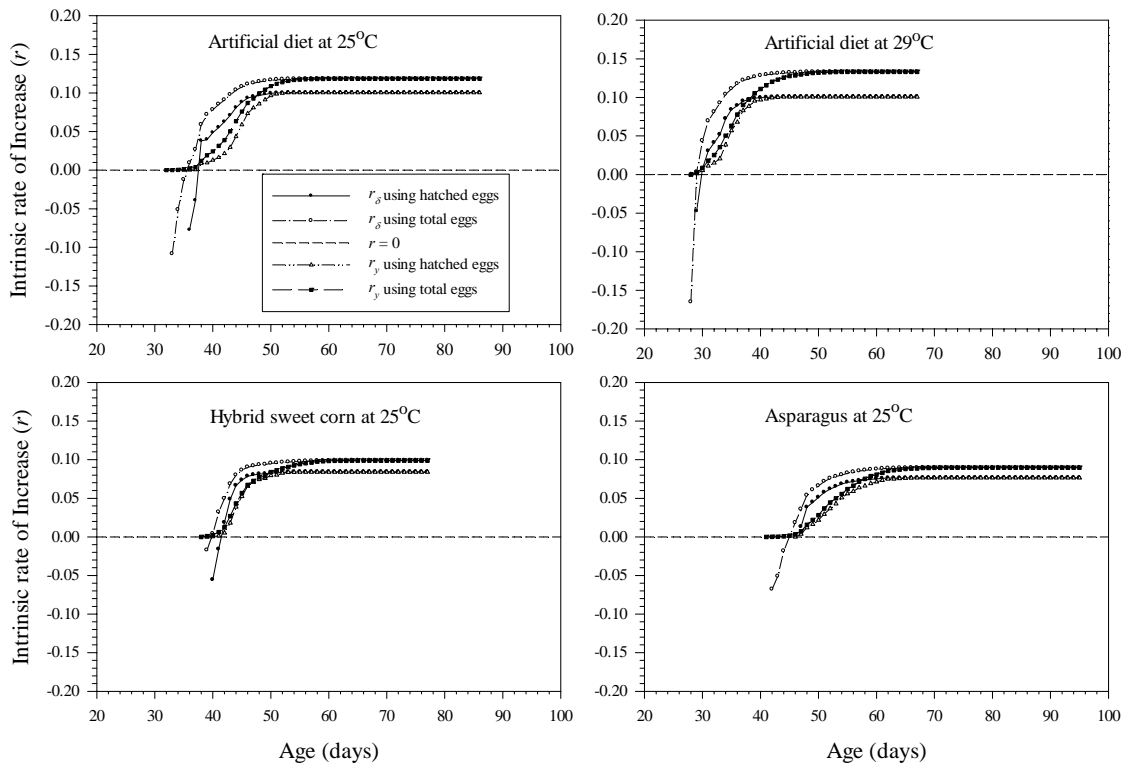


Fig. 3. The curtailed intrinsic rate ( $r_{\delta}$ ) and the cumulative contribution to the intrinsic rate ( $r_y$ ) for *Helicoverpa armigera* using the number of hatched eggs and the total number of eggs.

$$P_{post} = \left[ \frac{(y_{last} - y_{\delta, \max})}{y_{last}} \right] \times 100\%$$

Where  $y_{\delta, \max}$  is the age at which  $r_{\delta} = r$ , i.e. the last age of reproduction.

The curve of the cumulative contribution of an age ( $y$ ) to the intrinsic rate of increase ( $r_y$ ) for *H. armigera* reared at 25°C on artificial diet, hybrid sweet corn, and asparagus, and at 29°C on an artificial diet using total eggs and hatched eggs are also plotted in Fig. 3. The curve of  $r_y$  using total eggs also precedes the curve of  $r_y$  using hatched eggs. The original value of the intrinsic rate ( $r$ ) given in Table 2 was used as  $r$  in Eq. 3. The original values of the life table parameters given in Table 2 are the direct estimates

from the life table analysis before the mean and standard error estimation.

## Discussion

The survival and fecundity rates are the two basic life table data that make up the intrinsic rate of increase of an animal. Changes in survivorship and reproduction schedules result in changes in the intrinsic rate of increase. These changes can be examined by estimating the curtailed intrinsic rate of increase up to each age, while considering each age as a discard age. An intrinsic rate estimated to a particular age is referred to as the curtailed intrinsic rate. The discard age is the age beyond which the  $l_x$  and  $m_x$  data are discarded when estimating the curtailed intrinsic rate of increase. The

Table 1. Age at a specific category of the curtailed intrinsic rate and post-reproductive duration of *Helicoverpa armigera*

Condition	Age (y) (day) at			Last age of cohort (day)	post-reproductive duration $P_{post}$ (%)
	$r_{\delta-ve}$	$r_{\delta+ve}$	$r_{\delta_{max}}$		
Artificial diet at 25°C	36	38	55	85	35.3
Artificial diet at 29°C	29	30	47	66	28.8
Hybrid sweet corn at 25°C	40	42	55	76	27.6
Asparagus at 25°C	-	47	73	95	23.2

Table 2. Original estimates of the population parameters of *Helicoverpa armigera* using “hatched eggs” and “total eggs”

Population parameter (Original value)	Artificial diet at 29°C		Artificial diet at 25°C		Hybrid sweet corn at 25°C		Asparagus at 25°C	
	Hatched eggs	Total eggs	Hatched eggs	Total Eggs	Hatched eggs	Total eggs	Hatched eggs	Total eggs
	$n = 104$	$n = 120$	$n = 106$	$n = 120$	$n = 98$	$n = 120$	$n = 110$	$n = 130$
Intrinsic rate of increase ( $r$ ) (day <sup>-1</sup> )	0.1006	0.1330	0.1003	0.1183	0.0839	0.09873	0.0765	0.08958
Finite rate ( $\lambda$ ) (day <sup>-1</sup> )	1.1058	1.1423	1.1056	1.1256	1.0876	1.1038	1.0795	1.0937
Net reproductive rate ( $R_0$ ) (offspring)	40.0	178.3	104.5	243.5	50.1	117.1	67.4	146.5
Mean generation time ( $T$ ) (day)	36.7	39.0	46.3	46.4	46.6	48.2	55.1	55.7
Gross reproductive rate ( $GRR$ ) (offspring)	68.1	360.9	207.4	551.9	125.2	390.9	214.1	620.1

Note: The original estimates of the population parameters using hatched eggs for 29°C artificial diet, 25°C artificial diet and hybrid sweet corn were obtained from Jha *et al.* 2012 a & b and placed in the table for comparison.

curtailed intrinsic rate estimated in this manner reveals the biotic potentiality of a population surviving to a particular age. This makes for a comprehensive index that describes the effects of survivorship and fecundity on the intrinsic rate of increase of a population. This index is more useful for risk assessment in the conservation of endangered species (Chi and Su, 2006). It describes the effects of longevity on the survival probability and maternity of a population. Based on the life-table data of *H. armigera* reared at 25°C on an artificial diet, hybrid sweet corn, and asparagus, and at 29°C on an artificial diet, the curtailed intrinsic rates were estimated using the age-stage, two-

sex life table approach as depicted in Fig. 3. The upward shift of the curves of  $r_{\delta}$  estimated using the number total eggs are due to the very high  $m_x$  as a result of taking all eggs into account when estimating  $r_{\delta}$ .

The curves of  $r_{\delta}$  and  $r_y$  begin only when  $m_x > 0$  and reaches its highest value (=  $r$ ) (Table 2) when all females in the cohort have stopped laying eggs. The value of  $r_y$  ranges from zero to  $r$ . Cohen and Mackauer (1987) plotted the  $r_y$  to show that the older females of *Ephedrus californicus* Baker (Hymenoptera: Aphididae) contributes very little to the cohort growth rate. However, one should not confuse the cumulative contribution,  $r_y$  and the intrinsic

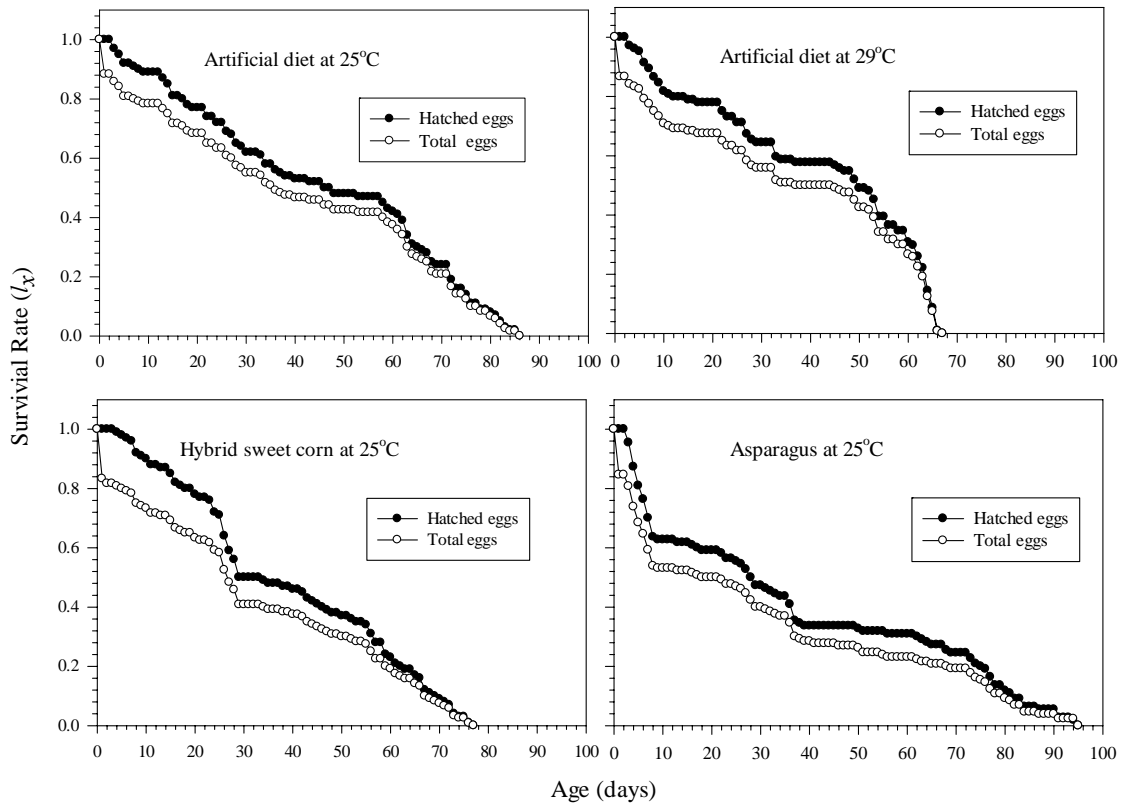


Fig. 4. The age-specific survival rate ( $l_x$ ) of *Helicoverpa armigera* calculated using 'hatched eggs' and 'total eggs'. The  $l_x$  curve using 'hatched eggs' at 29°C with an artificial diet, and at 25°C with an artificial diet and hybrid sweet corn (Jha *et al.* 2012 a and b) are shown for comparison.

rate,  $r$ , because they are two different measures. The cumulative contribution,  $r_y$  only provides a descriptive value of the cumulative input of individuals surviving to age  $y$  to the intrinsic rate,  $r$  (Chi and Su, 2006).

The sex ratio of the offspring is an important issue in the life table study (Huang and Chi 2011). The sex ratio is considered the principle index of the sex composition, and is usually defined as the number of males per female (Carey, 1993). Changes in the offspring sex ratio of an insect with female age is a phenomenon that can be observed in *H. armigera* (Fig. 2) as well as in other insects (Chi and Su, 2006) and mites (Hamilton *et al.*, 1986). In female age-specific life tables, a sex ratio

of 1:1 is usually assumed (Hoddle *et al.*, 2001; Legaspi and Legaspi, 2005; Mironidis and Savopoulou-Soultani, 2008; Nielsen *et al.*, 2008; Wang *et al.*, 2009; Chen and Parajulee, 2010; Soufbaf *et al.*, 2010). This may be either due to the difficulty in distinguishing the sexes during the pre-adult stage or as a result of not monitoring the sex ratios of the offspring produced by females at different ages. The sex composition in *H. armigera* is male-dominated, however, it achieves a 1:1 sex composition for a short period of time. When the adults begin to eclose from the pupal stage, the number of males per female is less than one (Fig. 2). This reduces the chance of mating and an unmated female may lay infertile eggs. A



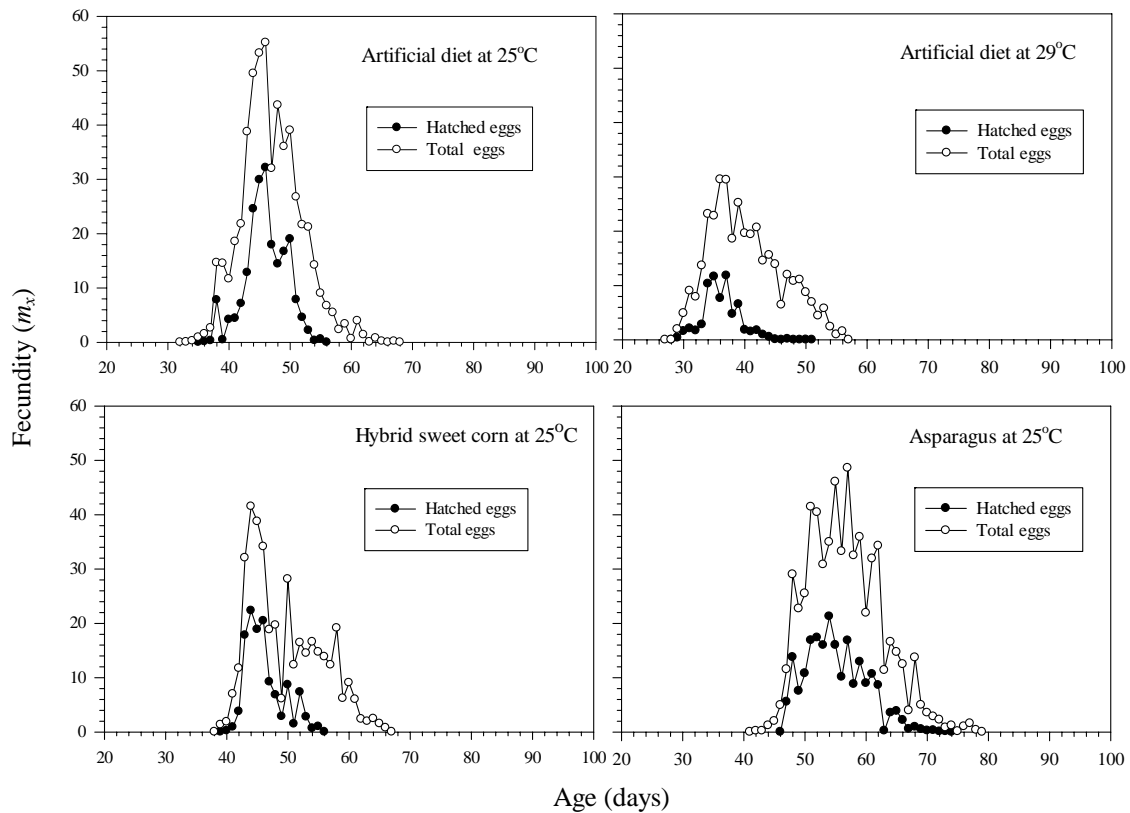


Fig. 5. The age-specific fecundity ( $m_x$ ) of *Helicoverpa armigera* calculated using 'hatched eggs' and 'total eggs'. The  $m_x$  curve using hatched eggs at 29°C with an artificial diet, and at 25°C with an artificial diet and hybrid sweet corn (Jha *et al.* 2012 a and b) are shown for comparison.

considerable number of females in a population of *H. armigera* have been reported to remain unmated (Liu *et al.*, 2004). In addition, a huge proportion of eggs laid by a mated female do not hatch (Fefelova and Frolov, 2008). The hatch rate varies with age-specific egg laying, as shown in Fig. 1. These variations in egg laying and their hatchability have many implications for the survivorship and fecundity schedule of *H. armigera*. The age-specific survival rate ( $l_x$ ) obtained using a fixed hatch rate and the total number of eggs shift the  $l_x$  curve downward (Fig. 4). Similarly, the age-specific fecundity ( $m_x$ ) obtained using the total number of eggs shift the  $m_x$  curve upward (Fig. 5). The age-specific survival

rate ( $l_x$ ) using hatched eggs in Fig. 4 and the age-specific fecundity ( $m_x$ ) using hatched eggs in Fig. 5 for 29°C on an artificial diet, and 25°C on an artificial diet, as well as sweet corn were taken from Jha *et al.* (2012a) and Jha *et al.* (2012b) and are shown as a comparison. To demonstrate these effects, an additional analysis of the life table at 29°C on an artificial diet and at 25°C on an artificial diet, sweet corn, and asparagus was conducted. This analysis included the unhatched eggs (i.e. used all laid-eggs) in the  $f_{xj}$  calculation and parent cohort, both with a fixed hatch rate (as observed in the beginning) of 86.67, 88.33, 81.7, and 84.6% respectively. The population parameters obtained from this analysis were

considerably higher than those estimated by using hatched eggs only (Table 2).

Thus, using a fixed hatch rate for all eggs and assuming a sex ratio (1:1) in the analysis of the life table of *H. armigera* (Liu *et al.*, 2004; Mironidis and Savopoulou-Soultani, 2008) could not reflect the actual biological phenomenon, and also led to an erroneous relationship between the net reproductive rate ( $R_0 = \sum_{x=0}^{\infty} l_x m_x$ ) and the mean female fecundity ( $F$ ) (Chi, 1988; Chi and Su, 2006; Jha *et al.*, 2012a) and overestimated the population parameters. The age-stage, two-sex life table takes the variation in sex ratio into due consideration when estimating the population parameters. We recommend the use of the age-specific number of viable eggs and the age-stage, two-sex life table theory in studying the life tables of insects and mites.

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# 存活率及繁殖率對玉米穗蟲 *Helicoverpa armigera* (Hübner) 內在增殖率的影響

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## 摘 要

本研究分析飼養於 25°C 人工飼料、甜玉米、蘆筍，以及 29°C 人工飼料的玉米穗蟲生命表，探討存活率與繁殖率對內在增殖率影響。縮減內在增殖率 (the curtailed intrinsic rate,  $r_s$ ) 顯示了存活率及繁殖率對內在增殖率的影響。利用年齡齡期兩性生命表理論去估算玉米穗蟲的縮減增殖率，其範圍由負值至正值，最終等同於內在增殖率。累計貢獻值 (the cumulative contribution,  $r_y$ ) 則為個體存活至年齡  $y$  時對內在增殖率貢獻的描述值。累計貢獻值 ( $r_y$ ) 的範圍由 0 至  $r$ ，但其並非一內在增殖率。使用固定卵孵化率開始進行玉米穗蟲生命表研究時，群體包含未受精卵，忽略卵孵化率而利用總產卵數計算繁殖率時，無法反應出玉米穗蟲真正的生物學特性。更確切的說，此方式會降低存活曲線、提高繁殖曲線，並導致估算出非常高的生命表族群參數，這將會降低使用內在增殖率評估玉米穗蟲在不同環境條件下適存性的可信度。因此，我們建議使用孵化卵數計算繁殖率。此外，在數據分析上應使用年齡齡期兩性命表以便能更精準地包含性比率、卵孵化率及發育隨年齡之變化。

**關鍵詞：**玉米穗蟲、性比、孵化率、縮減增殖率。

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