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## Life Table of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) with a Discussion on Jackknife vs. Bootstrap Techniques and Variations on the Euler-Lotka Equation **【Research report】**

### 利用玉米穗蟲*Helicoverpa armigera* (Hübner) 的生命表與Jackknife和Bootstrap方法之討論與Euler-Lotka Equation的變異 **【研究報告】**

Ratna K. Jha<sup>1,2</sup>, Hsin Chi<sup>1</sup>, and Li-Cheng Tang<sup>1\*</sup>

陳樂<sup>1,2</sup>、齊心<sup>1</sup>、唐立正<sup>1\*</sup>

\*通訊作者E-mail: [ictang@dragon.nchu.edu.tw](mailto:ictang@dragon.nchu.edu.tw)

Received: 2012/06/05 Accepted: 2012/06/18 Available online: 2012/12/01

#### Abstract

Life table data for *Helicoverpa armigera* (Hübner) that were reared on an artificial diet at 29°C were collected in the laboratory and analyzed using the age-stage, two-sex life table. The age-specific fecundity was calculated based on the number of eggs hatched in order to accurately reveal the biological characteristics of *H. armigera* by capturing the variation in hatch rate with female age. The intrinsic rate of increase ( $r$ ), finite rate ( $\lambda$ ) and mean generation time ( $T$ ), net reproductive rate ( $R_0$ ), and gross reproductive rate (GRR) of *H. armigera* were 0.1029 d<sup>-1</sup>, 1.1083 d<sup>-1</sup>, 36.7 d, 40.2 offspring and 68.6 offspring, respectively. The relationship between the net reproductive rate and the mean female fecundity was consistent with theoretical proof. This study indicated that a 29°C temperature regime is not as conducive as a 25°C temperature regime for rearing *H. armigera* on an artificial diet in the laboratory. The standard errors of the life table parameters were estimated using both the jackknife and bootstrap techniques. The frequency distribution of the sample means obtained by the jackknife technique failed the normality test, while the bootstrap results fitted the normal distribution well. Because the jackknife technique generates biologically meaningless zeros for the net reproductive rate, it should not be used for estimating the standard error of the net reproductive rate. The application of the jackknife technique in estimating other population parameters requires further examination. For a correct estimation of the intrinsic rate, the age index and the exponent in the Euler-Lotka equation should be chosen according to the definition of the age-specific survival rate ( $l_x$ ) and the age-specific fecundity ( $m_x$ ). Because the age-stage, two-sex life table accurately describes the survival, development, stage differentiation, and reproduction of insects, we suggest it should be used in the analysis of insect demography.

#### 摘要

本研究以年齡齡期兩性生命表理論分析玉米穗蟲*Helicoverpa armigera* (Hübner) 在實驗室29°C的環境條件下取食人工飼料之生命表。以孵化卵數計算年齡別繁殖率可正確呈現不同日齡雌蟲所產的卵之孵化率的變化，並準確的呈現玉米穗蟲的生物學特性。玉米穗蟲的內在增殖率 ( $r$ )、終極增殖率 ( $\lambda$ )、平均世代時間 ( $T$ )、淨增殖率 ( $R_0$ ) 以及粗繁殖率 (GRR) 分別為0.1029 d<sup>-1</sup>、1.1083 d<sup>-1</sup>、36.7 d、40.2 offspring以及68.6 offspring；淨增殖率及雌蟲平均繁殖力間的關係與理論證明相符。本研究指出，以人工飼料飼養玉米穗蟲的方式在29°C的環境條件並不如25°C下有利。利用jackknife和bootstrap兩種方法估計生命表族群參數的變方與標準誤差，以jackknife重新取樣的方法所得到的pseudo values之頻率分布在常態檢定下是失敗的，但bootstrap的結果符合常態分布檢定。因為在使用jackknife方法時會產生沒有生物學意義的淨增殖率為零的pseudo values，因此jackknife的方式不應該用來估算淨增殖率的標準誤差。jackknife應用在其他族群參數的估算上需要有更進一步的探討。為了正確估算內在增殖率，Euler-Lotka方程式中的年齡標示必須符合存活率和繁殖率所定義的年齡標示。由於年齡齡期兩性生命表準確描述昆蟲的存活、發育、齡期分化以及繁殖，我們建議昆蟲的生命表分析應使用兩性生命表。

**Key words:** *Helicoverpa armigera*, intrinsic rate of increase, Euler-Lotka formula, jackknife, bootstrap

**關鍵詞:** 人口統計學、內在增殖率、Euler-Lotka方程式、Jackknife、Bootstrap。

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# Life Table of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) with a Discussion on Jackknife vs. Bootstrap Techniques and Variations on the Euler-Lotka Equation

Ratna K. Jha<sup>1,2</sup>, Hsin Chi<sup>1</sup>, and Li-Cheng Tang<sup>1\*</sup>

<sup>1</sup> Department of Entomology, National Chung Hsing University, Taichung 40227, Taiwan

<sup>2</sup> Plant Protection Directorate, Department of Agriculture, Hariharbhawan, Lalitpur, Nepal

## ABSTRACT

Life table data for *Helicoverpa armigera* (Hübner) that were reared on an artificial diet at 29°C were collected in the laboratory and analyzed using the age-stage, two-sex life table. The age-specific fecundity was calculated based on the number of eggs hatched in order to accurately reveal the biological characteristics of *H. armigera* by capturing the variation in hatch rate with female age. The intrinsic rate of increase ( $r$ ), finite rate ( $\lambda$ ) and mean generation time ( $T$ ), net reproductive rate ( $R_0$ ), and gross reproductive rate ( $GRR$ ) of *H. armigera* were 0.1029 d<sup>-1</sup>, 1.1083 d<sup>-1</sup>, 36.7 d, 40.2 offspring and 68.6 offspring, respectively. The relationship between the net reproductive rate and the mean female fecundity was consistent with theoretical proof. This study indicated that a 29°C temperature regime is not as conducive as a 25°C temperature regime for rearing *H. armigera* on an artificial diet in the laboratory. The standard errors of the life table parameters were estimated using both the jackknife and bootstrap techniques. The frequency distribution of the sample means obtained by the jackknife technique failed the normality test, while the bootstrap results fitted the normal distribution well. Because the jackknife technique generates biologically meaningless zeros for the net reproductive rate, it should not be used for estimating the standard error of the net reproductive rate. The application of the jackknife technique in estimating other population parameters requires further examination. For a correct estimation of the intrinsic rate, the age index and the exponent in the Euler-Lotka equation should be chosen according to the definition of the age-specific survival rate ( $l_x$ ) and the age-specific fecundity ( $m_x$ ). Because the age-stage, two-sex life table accurately describes the survival, development, stage differentiation, and reproduction of insects, we suggest it should be used in the analysis of insect demography.

**Key words:** *Helicoverpa armigera*, intrinsic rate of increase, Euler-Lotka formula, jackknife, bootstrap

## Introduction

*Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) is an agricultural pest of worldwide significance. It achieved pest status partly due to its polyphagy, high mobility, high fecundity, and facultative diapause, which enables it to survive in various habitats and adapt to seasonal changes (Fitt, 1989). It is listed as a quarantine pest by the European and Mediterranean Plant Protection Organization (EPPO, 2008). Larvae of *H. armigera* prefer to eat the reproductive organs of plants (Zalucki *et al.*, 1986; Fitt, 1989). Temperature is one of the most important abiotic factors that influence the survivorship, development and reproduction of this species (Mironidis and Savopoulou, 2008). However, being an ectothermic animal, insects can rapidly acclimatize (Yazdani and Agrawal, 1997).

Despite an enormous volume of research work done on *H. armigera* (Fitt, 1989), the published studies that focused on the ecology of this pest are rather small (Zalucki *et al.*, 1986). Diverse types of ecological studies have used life table analysis in their research (Wilcox and Murphy, 1985; Chi and Getz, 1988; Chi, 1990; Bellows *et al.*, 1992; Chi, 1994; Sakai *et al.*, 2001; Stark and Banks, 2003). Life table analysis is an effective way to accurately comprehend the effect of external factors on the growth, survival, reproduction, and the intrinsic rate of increase of insect populations (Chi and Su, 2006). Thus, in order to develop a better understanding of the variation in demography of this pest, it is necessary to develop accurate life tables for *H. armigera* under different conditions (Zalucki *et al.*, 1986). Understanding the demography of an insect under variable conditions is the cornerstone for developing strategy to manage it in an eco-friendly manner.

Some life history studies of *H. armigera* have been performed under varying conditions (Jallow *et al.*, 2001; Pascua and

Pascua, 2002; Ge *et al.*, 2003; Liu *et al.*, 2004; Wu *et al.*, 2006; Fu *et al.*, 2008; Mironidis and Savopoulou, 2008; Yin *et al.*, 2009, 2010; Naseri *et al.*, 2009, 2011; Jha *et al.*, 2012). Many of these studies are based on age-specific, female-only life tables, which ignore the stage overlapping in *H. armigera* populations (e.g., Liu *et al.*, 2004), or calculate age-specific fecundity based on the "adult age" (e.g., Mironidis and Savopoulou, 2008). Some studies are based on partial life tables (e.g., van denBerg and Cock, 1993; Dabhi and Patel, 2007). Like most insects, *H. armigera* populations are two-sex with considerable variation in the developmental rate among individuals, in offspring sex ratio and in the hatch rate of eggs produced by mothers of different ages (Jha *et al.*, 2012). The application of an age-specific female life table (Lewis, 1942; Leslie, 1945; Birch, 1948) to *H. armigera* leads to an erroneous relationship among gross reproductive rate, net reproductive rate, and pre-adult survivorship (Yu *et al.*, 2005; Jha *et al.*, 2012). The application of the age-stage, two-sex life table theory (Chi and Liu, 1985; Chi, 1988) overcomes such shortfalls when estimating life table parameters. The jackknife and bootstrap techniques are usually used to estimate the variance of life table parameters to correct for bias. Efron (1982) reported that the bootstrap technique has a higher reliability than the jackknife technique for estimating variances. Although the jackknife technique has been used in demographic statistics for several decades, Chi and Yang (2003) noticed the problem and explicitly stated that "It results in some degree of discrepancy between the estimated means and their definition".

In this study, the life history data of *H. armigera* reared on an artificial diet at 29°C were collected and analyzed using the age-stage, two-sex life table theory. Since 29°C is a candidate temperature used for rearing *H. armigera* in the laboratory, the demographic merits and

demerits of rearing *H. armigera* at 29°C were evaluated against the demography of *H. armigera* reared at 25°C as mentioned in Jha *et al.* (2012). In the present paper we demonstrated the procedure of jackknife and bootstrap techniques extended to a net reproductive rate and discussed its applicability. The accuracy of the various forms of the basic demographic equation, i.e. the Euler-Lotka equation, ever debated (David, 1995; Case, 2000), is also illustrated by calculations from the data of a hypothetical cohort to solve for  $r$ , and the result was cross-checked with the result obtained from the Lewis-Leslie matrix and the population projection.

## Materials and Methods

***Helicoverpa armigera*:** A colony of *H. armigera* was originally collected from a field in Taichung City and maintained in the Microbial Control Laboratory, Department of Entomology, National Chung Hsing University, Taichung, Taiwan (R.O.C.). The colony was periodically supplemented with larvae collected from the field to reduce inbreeding depression. The colony was maintained on an artificial diet at 25°C. The composition of the artificial diet was modified from Kao (1995). The ingredients of this diet were the same as those mentioned in Jha *et al.* (2012).

**Life table study.** The colony of *H. armigera* was reared on the artificial diet for one generation in a growth chamber at  $29 \pm 1^\circ\text{C}$ ,  $65 \pm 5\%$  RH, and a photoperiod of 14:10 (L:D) prior to the life table study. Newly emerged adults were paired and kept in pairs in an individual oviposition container (a plastic cup measuring 9 cm in diameter  $\times$  5.5 cm in height, lined with paper towel). The adults were provided each day with a 30% honey solution soaked in a cotton ball. Eggs from each female were collected in Petri dishes (9 cm diameter) and kept separately in the growth chamber mentioned above. The hatch rate was observed daily. Due to the

variable hatch rate of eggs laid by females of different ages, we used 112 hatched first instars with known egg duration to begin the life table study. The newly hatched larvae were individually transferred to Petri dishes (9 cm diameter) by using a fine brush. They were then reared as a group to second instar. The third and older instars were reared individually in 30-well plates. The individual larvae were observed daily for molting and survivorship. The artificial diet was replaced every other day. The larvae entering 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  $\times$  5.5 cm height). Newly emerged adults were paired in oviposition containers lined with paper towel and transferred daily to a new container. Eggs laid by each female at different ages were collected and kept separately to record the hatch rates. If any moth died earlier than its mate, an individual of the same sex would be supplied from the mass reared colony. The data from these recruited individuals were excluded from the analysis.

**Data analysis.** We analyzed the raw data based on the theory of the age-stage, two-sex life table (Chi and Liu, 1985) and the method described by Chi (1988). The mean of the development periods for each development stage, the longevity of each adult male and female, the adult pre-oviposition period (APOP), the total pre-oviposition period (TPOP) and the female fecundity of *H. armigera* were calculated. The APOP was calculated based on the adult age, while the TPOP took the total pre-adult age into consideration. The age-stage specific survival rate ( $s_{xj}$ ) (where  $x$  is the age and  $j$  is the stage), the age-stage specific fecundity ( $f_{xj}$ ), the age-specific survival rate ( $l_x$ ), and the age-specific fecundity ( $m_x$ ) were calculated from daily records of survival and

fecundity of all the individuals of the cohort. The  $s_{xj}$  is the probability that a new born will survive to age  $x$  and stage  $j$ . The age-specific survival rate ( $l_x$ ) is the probability that a new born survives to age  $x$ , and was calculated as  $l_x = \sum_{j=1}^m s_{xj}$  where  $m$  is the number of stages. The age-specific fecundity ( $m_x$ ) was calculated from the daily records of the survival and fecundity of all individuals in the cohort ( $m_x = \left[ \sum_{j=1}^m s_{xj} f_{xj} \right] / \sum_{j=1}^m s_{xj}$ ). 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, the  $f_{xj}$  was calculated from the number of eggs that hatched, because it reflects the true biological characteristics of *H. armigera*. The population parameters estimated were the intrinsic rate of increase ( $r$ ), the finite rate ( $\lambda$ ), the gross reproductive rate ( $GRR$ ), the net reproductive rate ( $R_0$ ), and the mean generation time ( $T$ ). In this paper, the intrinsic rate of increase was estimated by using the iterative bisection method from the Euler-Lotka formula:

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

with the age indexed from 0 (Goodman, 1982). The finite rate  $\lambda$  was calculated as  $e^r$ . The mean generation time ( $T$ ) is defined as the length of time that a population needs to increase to  $R_0$ -fold of its size when the stable age-stage distribution and the stable increase rate (i.e.,  $r$  and  $\lambda$ ) are reached. In other words, this means that  $e^{rT} = R_0$  or  $\lambda^T = R_0$ . The mean generation time was calculated as  $T = \ln R_0 / r$ . The net reproductive rate ( $R_0$ ) was calculated as  $R_0 = \sum_{x=0}^{\infty} l_x m_x$ . The gross reproductive rate ( $GRR$ ) was calculated as  $GRR = \sum m_x$ . Based on the age-stage, two-sex life table, the life expectancy for an individual of age  $x$  and stage  $y$  ( $e_{xy}$ ) was calculated as follows,

$$e_{xy} = \sum_{i=x}^n \sum_{j=y}^m s'_{ij} \quad 2$$

where  $n$  is the number of age groups,  $m$  is the number of stages, and  $s'_{ij}$  is the probability that an individual of age  $x$  and stage  $y$  will survive to age  $i$  and stage  $j$  respectively, and is calculated by assuming that  $s'_{xy} = 1$  following the procedures described in Chi (1988) and Chi and Su (2006). The age-stage specific reproductive value ( $v_{xj}$ ) (where  $x$  is the age and  $j$  is the stage) was calculated as well. As we begin the life table with newly hatched larvae with known egg duration, and since the unhatched eggs were excluded from the parent cohort we also excluded the unhatched eggs from the fecundity in the life table analysis. Eight individuals that died due to mechanical damage or disappeared during the experiment were also excluded from the analysis. To deal with the tedious process of raw data analysis and to achieve high accuracy in the parameter estimation, we used a computer program, TWSEX-MSChart for age-stage, two-sex life-table analysis (Chi, 2012a), designed in Visual BASIC (Version 6.0 Service pack 6) for the Windows operating system, available at <http://140.120.197.173/Ecology/prod02.html> (National Chung Hsing University, Taichung, Taiwan). The population parameters, development times, and fecundities of *H. armigera* reared at 29°C were compared with the cohort reared at 25°C by re-analyzing the raw data set of the life table from Jha *et al.* (2012). Since a normal distribution is a prerequisite for the application of the  $t$ -test, the Mann-Whitney test ( $U$ -test) (Sigmaplot 11.0, Systat Software Inc.) was used to perform the significance test of the variables due to the failure of the data in the normality test.

In this study, the procedure of Meyer *et al.* (1986) and Efron and Tibshirani (1993) were adopted for the jackknife and

bootstrap techniques in order to estimate the means and standard errors of the intrinsic rate of increase ( $r$ ), the finite rate ( $\lambda$ ), the gross reproductive rate ( $GRR$ ), the net reproductive rate ( $R_0$ ) and the mean generation time ( $T$ ). The frequency distribution curves of the net reproductive rate ( $R_0$ ) estimated using these two resampling techniques were compared. Meyer *et al.* (1986) mentioned the step by step procedure for applying these two resampling techniques only to the intrinsic rate of increase ( $r$ ). In the next sections, the procedure for applying these two techniques to the net reproductive rate ( $R_0$ ) will be described step by step.

**Jackknife Procedure.** First of all, in order to apply the jackknife technique to the net reproductive rate ( $R_0$ ), the net reproductive rate for all  $n$  individuals of the cohort ( $R_{0,all}$ ) must be calculated as

$$R_{0,all} = \sum_{x=0}^{\infty} l_x m_x \quad 3$$

where  $l_x$  and  $m_x$  are calculated by including all individuals in the cohort. Then, an individual  $i$  is omitted and the other  $n-1$  individuals are used to calculate the jackknife value of  $R_{0,i}$  as

$$R_{0,i} = \sum_{x=0}^{\infty} l_x m_x \quad 4$$

where  $l_x$  and  $m_x$  are calculated by omitting the data for individual  $i$ . In the next step,  $R_{0,i-pseudo}$  is calculated as

$$R_{0,i-pseudo} = n \cdot R_{0,all} - (n-1) \cdot R_{0,i} \quad 5$$

Finally, according to the jackknife technique the mean  $R_{0,J}$ , variance  $s_{J,}^2$  and the standard error  $se(R_{0,J})$  are calculated as

$$R_{0,J} = \frac{\sum_{i=1}^n R_{0,i-pseudo}}{n} \quad 6$$

$$s_J^2 = \frac{\sum_{i=1}^n (R_{0,i-pseudo} - R_{0,J})^2}{n-1} \quad 7$$

$$se(R_{0,J}) = \sqrt{\frac{s_J^2}{n}} \quad 8$$

**Bootstrap procedure.** In the bootstrap procedure, a sample of  $n$  individuals from the cohort is taken with replacement and  $R_{0,i-boot}$  is then calculated for the bootstrap sample as

$$R_{0,i-boot} = \sum_{x=0}^{\infty} l_x m_x \quad 9$$

where the subscript  $i-boot$  represents the  $i$ th bootstrap and  $l_x$  and  $m_x$  are calculated from the  $n$  individuals selected randomly with replacement. In this paper, this procedure was repeated 10,000 times ( $m = 10,000$ ). We then computed the bootstrap estimates of the mean  $R_{0,B}$ , variance  $s_B^2$  and standard error  $se(R_{0,B})$  of the net reproductive rate as

$$R_{0,B} = \frac{\sum_{i=1}^m R_{0,i-boot}}{m} \quad 10$$

$$s_B^2 = \frac{\sum_{i=1}^m (R_{0,i-boot} - R_{0,B})^2}{m-1} \quad 11$$

$$se(R_{0,B}) = \sqrt{\frac{s_B^2}{m}} \quad 12$$

Following the same procedures for the corresponding estimates of the gross reproductive rate ( $GRR$ ), the mean  $GRR_J$ , variance and standard error of  $GRR_J$ , according to jackknife techniques and the mean  $GRR_B$ , the variance and standard

Table 1. Basic statistics (mean  $\pm$  S.E.) of the life history of *Helicoverpa armigera* reared at 29°C

Statistics	Stage or Sex	Temperature Regime				<i>p</i>
		29°C		25°C <sup>†</sup>		
		<i>n</i>	Mean $\pm$ S.E.	<i>n</i>	Mean $\pm$ S.E.	
Stage specific pre- adult duration (d)	Egg	104	2.08 $\pm$ 0.03	106	2.53 $\pm$ 0.05	<0.001
	First Instar	100	2.22 $\pm$ 0.05	97	2.4 $\pm$ 0.05	0.007
	Second Instar	93	2.15 $\pm$ 0.1	89	3.38 $\pm$ 0.09	<0.001
	Third Instar	83	3.66 $\pm$ 0.21	81	4.95 $\pm$ 0.30	<0.001
	Fourth Instar	82	2.96 $\pm$ 0.14	77	4.04 $\pm$ 0.28	0.001
	Fifth Instar	82	3.11 $\pm$ 0.16	74	4.89 $\pm$ 0.16	<0.001
	Sixth Instar	45	3.53 $\pm$ 0.21	7	3.71 $\pm$ 0.36	0.477
	Larva	80	16.01 $\pm$ 0.35	74	19.58 $\pm$ 0.49	<0.001
	Prepupa	77	2.31 $\pm$ 0.06	71	2.20 $\pm$ 0.10	0.323
	Pupa	62	9.95 $\pm$ 0.15	60	12.77 $\pm$ 0.19	<0.001
	Egg- Pupa	62	29.97 $\pm$ 0.4	60	37.10 $\pm$ 0.60	<0.001
Pupal weight (gm)	Pupa	62	0.249 $\pm$ 0.006	60	0.261 $\pm$ 0.005	0.145
Adult longevity (d)	Female	30	28.03 $\pm$ 1.05	29	30.17 $\pm$ 2.88	0.249
	Male	32	28.88 $\pm$ 1.69	31	27.68 $\pm$ 2.02	0.659
APOP (d)	Female	14	5.34 $\pm$ 0.73	19	7.16 $\pm$ 0.89	0.218
TPOP (d)	Female	14	35.36 $\pm$ 1.12	19	42.37 $\pm$ 0.58	<0.001
Fecundity ( <i>F</i> ) (eggs/female)	Female	30	138.7 $\pm$ 49.4	29	381.8 $\pm$ 104.7	0.077
Oviposition days	Female	14	5.07 $\pm$ 0.34	19	7.32 $\pm$ 0.29	0.254

<sup>†</sup> Data are from the same source used for Jha *et al.* (2012)

All the *p* values are obtained from the *U*-test except for the *p* value of the pupal weight.

APOP (Adult pre-oviposition period) and TPOP (Total pre-oviposition period) are calculated by using females that produced fertile eggs.

The mean oviposition days are calculated by taking only those days in which the number of hatched eggs was more than zero.

error of  $GRR_B$ , according to the bootstrap technique, are then estimated.

## Results

The development times for each stage, adult longevity, pre-oviposition period, and female fecundity of *H. armigera* at 29°C are listed in Table 1. The duration of each stage of *H. armigera* reared at 29°C was significantly shorter than for individuals reared at 25°C with the exception of the 6<sup>th</sup> larval instar and prepupa. When reared at 29°C, 55% of the 5<sup>th</sup> instar larvae developed to 6<sup>th</sup> instars, while only 9% of the 5<sup>th</sup> instars reared at 25°C developed to 6<sup>th</sup> instars. There was no

significant difference in pupal weight between *H. armigera* reared at 29°C and individuals reared at 25°C (Table 1). The mean total pre-oviposition period (TPOP) of *H. armigera* reared at 29°C was 35.36 days, which is significantly shorter than for individuals reared at 25°C. The mean fecundity of *H. armigera* at 29°C was 138.73 fertile eggs which is considerably less than the mean fecundity of *H. armigera* reared at 25°C (381.79 fertile eggs). The percentage of oviposition days was 18.09% when reared at 29°C and 24.25% when reared at 25°C. The age-specific total number of eggs and number of hatched eggs are shown in Fig. 1.

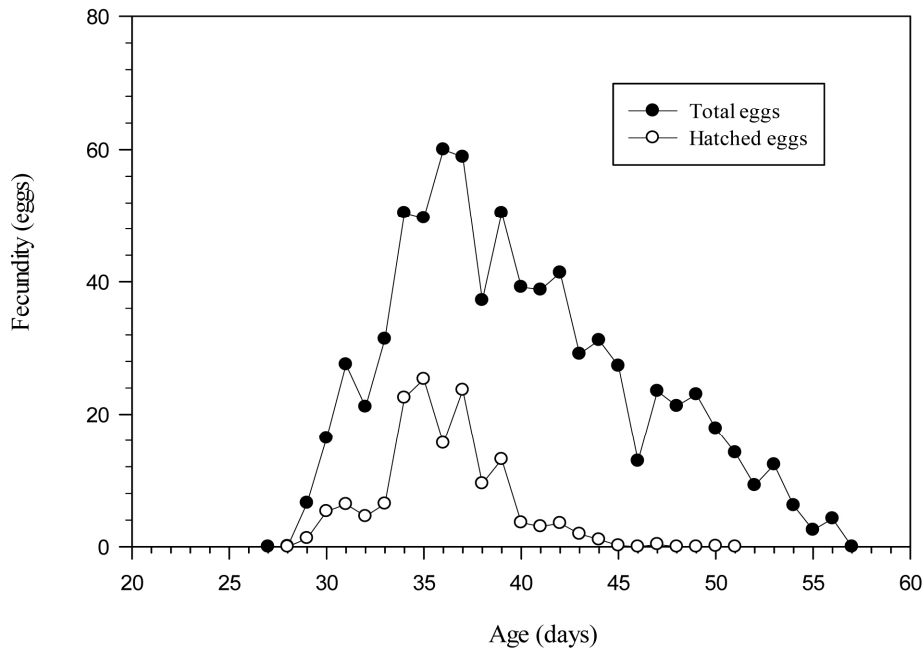


Fig. 1. Age-specific total number of eggs laid and age-specific hatched eggs of *Helicoverpa armigera* reared at 29°C.

The age-stage survival rate ( $s_{xj}$ ) of *H. armigera* reared at 29°C is plotted in Fig. 2. Parameter  $s_{xj}$  is the probability that a new born of *H. armigera* will survive to age  $x$  and stage  $j$ . The variable development rates among individuals in the cohort resulted in an overlapping of the stage-specific survivorship curves. The daily mean number of fertile eggs produced by individual *H. armigera* of age  $x$  and stage  $j$  is shown with the female age-stage specific fecundity ( $f_{xj}$ ) (Fig. 3). Because only female adults (the ninth life history stage) produce offspring, there is only a single curve of the female age-stage specific fecundity ( $f_{x9}$ ). When all individuals of age  $x$  are included, it is expressed as the age-specific fecundity of the total population ( $m_x$ ). Parameter  $l_x$  describes the change in the survival rate of the cohort with age (Fig. 3). It is the simplified version of the  $s_{xj}$  curves shown in Fig. 2. The product of  $l_x$  and  $m_x$  is the age-specific maternity ( $l_x m_x$ ) of *H. armigera*. Lower peaks of  $f_{x9}$ ,  $m_x$  and  $l_x m_x$  were

observed for *H. armigera* reared at 29°C than for *H. armigera* reared at 25°C (Fig. 3 of Jha *et al.*, 2012).

The age-stage life expectancy ( $e_{xj}$ ) (where  $x$  is the age and  $j$  is the stage) shows the expected lifespan for an individual of age  $x$  and stage  $j$  (Fig. 4). The age-stage life expectancy of the cohort of *H. armigera* reared at 29°C was shorter than the cohort reared at 25°C (Fig. 4 of Jha *et al.*, 2012). The contribution of an individual of age  $x$  and stage  $j$  to the future population is shown by the reproductive value ( $v_{xj}$ ) (Fig. 5) (Fisher, 1930).

The means and standard errors of  $r$ ,  $\lambda$ ,  $R_0$ ,  $GRR$ , and  $T$  that were estimated by using the jackknife method and the bootstrap method are listed in Table 2. The intrinsic rate of increase and the finite rate ( $\lambda$ ) for *H. armigera* at 29°C were 0.1029 d<sup>-1</sup> and 1.1083 d<sup>-1</sup>, respectively. At 29°C,  $R_0$ ,  $T$  and  $GRR$  for *H. armigera* were 40.2 offspring, 36.7 d, and 68.6 offspring, respectively. Comparing the bootstrap



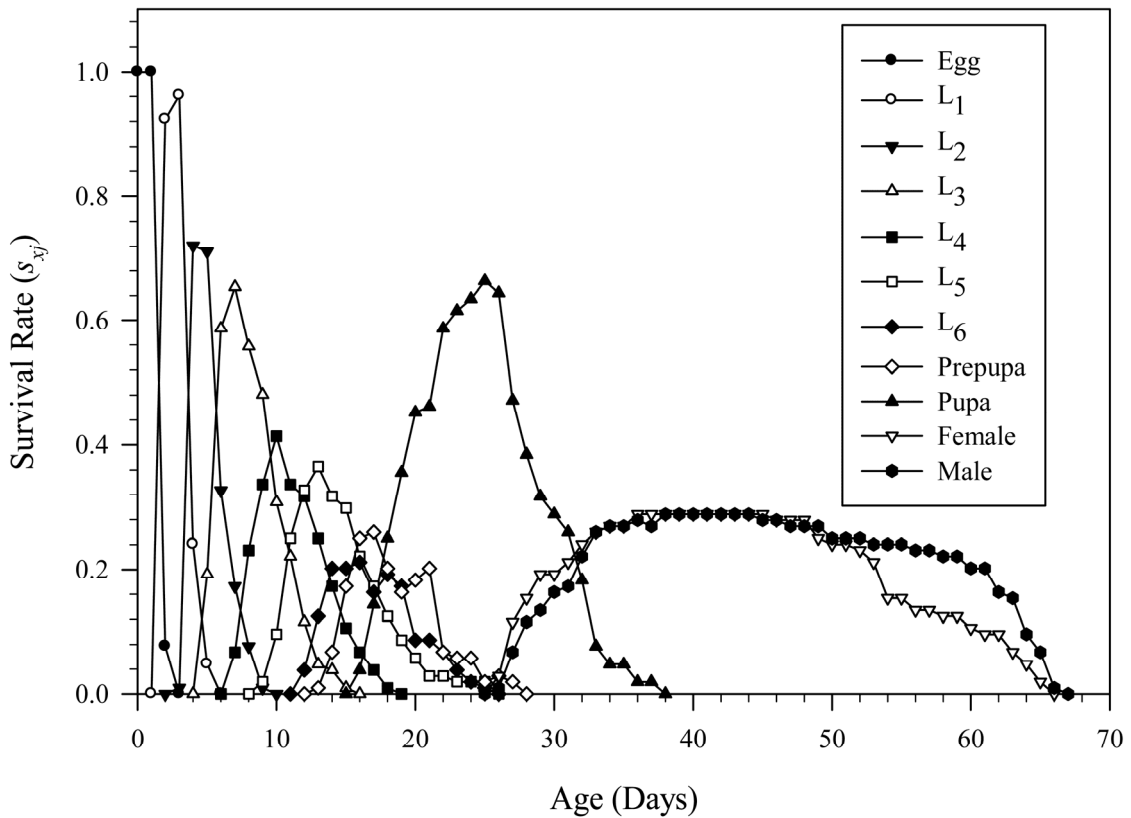


Fig. 2. Age-stage specific survival rate ( $s_{xj}$ ) of *Helicoverpa armigera* reared at 29°C.

results shows that  $R_0$  and  $GRR$  for *H. armigera* reared at 29°C were significantly lower than those for the cohort reared at 25°C. However, there were significant differences in  $r$  and  $\lambda$  in the jackknife estimation (Table 2). The mean generation time ( $T$ ) was significantly different in both cases. For all population parameters, the variance estimated by the jackknife technique is much higher than that estimated by the bootstrap technique. The relationship between the mean fecundity and the net reproductive rate estimated by the bootstrap technique was, however, slightly inconsistent with the relationship proved by mathematical method in Chi and Su (2006). This observation tells us that we must take particular caution when applying resampling methods such

as the jackknife and the bootstrap.

## Discussion

This study comprehensively presented the life history and demography of *H. armigera* reared at 29°C. The shorter pre-adult stage, adult longevity and oviposition periods of *H. armigera* at 29°C in comparison to 25°C indicate a higher developmental rate at higher temperature. The basic statistics are consistent with the findings of Mironidis and Savopoulou-Sultani (2008).

The age-stage, two-sex life theory has been widely applied in the study of various ecological aspects of insect pests and their natural enemies (Gabre *et al.*, 2005; Amir-Maafi and Chi, 2006; Mo and Liu, 2006; Silva *et al.*, 2006; Yang and Chi, 2006; Tsai

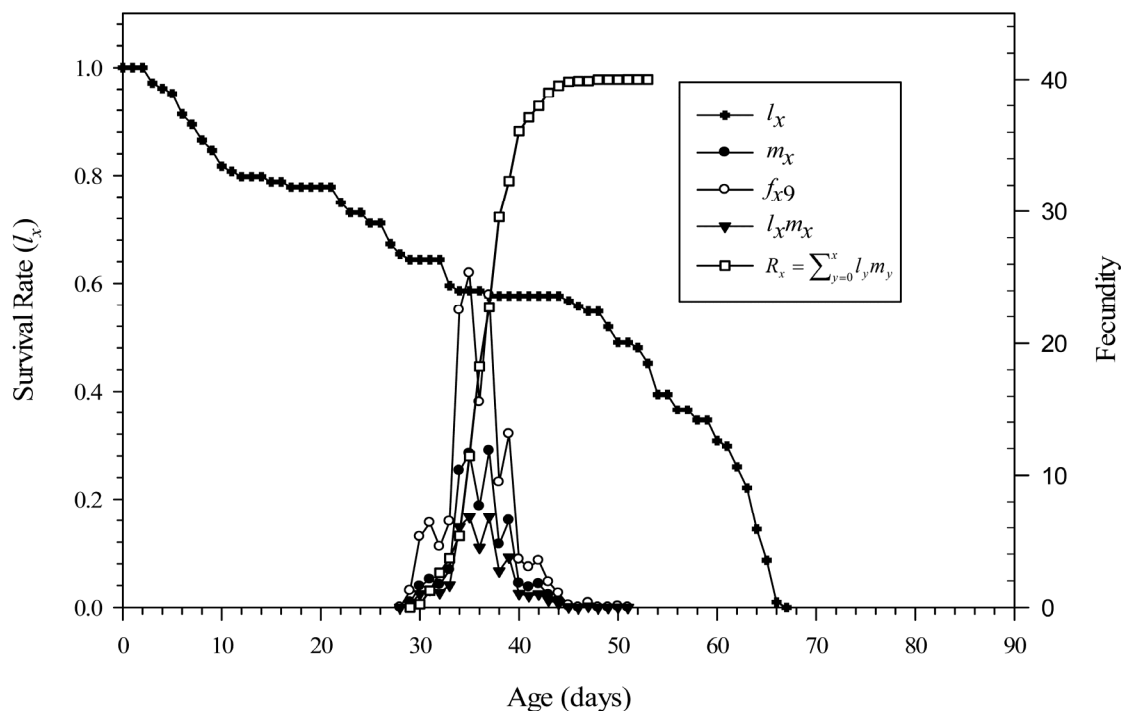


Fig. 3. Age-specific survival rate ( $l_x$ ), female age-specific fecundity ( $f_{x9}$ ), age-specific fecundity of the total population ( $m_x$ ), age-specific maternity ( $l_x m_x$ ) and cumulative reproductive rate ( $R_x$ ) of *Helicoverpa armigera* reared at 29°C.

and Chi, 2007; Atlihan and Chi, 2008; Kavousi *et al.*, 2009; Schneider *et al.*, 2009; Bailey *et al.*, 2010; Gao *et al.*, 2012; Han *et al.*, 2012; He *et al.*, 2012; Nguyen and Shih, 2012; Seyed-Talebi *et al.*, 2012). The age-stage, two-sex life table can reveal the actual life history of *H. armigera*. For example, the overlapping in the  $s_{xj}$  curves (Fig. 2), in the  $e_{xj}$  curves (Fig. 4), and in the  $v_{xj}$  curves (Fig. 5) are due to the incorporation of the variable developmental rates among individuals into the age-stage, two-sex life table. Many researchers constructed the survival curves based on the means of each stage or adult age (e.g., Marcic, 2003, 2005; Legaspi, 2004; Kontodimas and Stathas, 2005; Legaspi and Legaspi, 2005; Lin and Ren, 2005; Kivan and Kilic, 2006; Tsoukanas *et al.*, 2006). Lack of knowledge of the variable developmental rate will generate errors in the survival

and fecundity curves and the overlapping in the stage-specific survival curves can not be properly presented. For example, there were a number of errors in Sandhu *et al.* (2010). On page 2028, the survival curve ( $l_x$ ) of Fig. 1h shows  $l_3 > l_2$ . Because the survival rate ( $l_x$ ) must be a decreasing sequence of age, it, by definition, must be in the format  $1 \geq l_1 \geq l_2 \geq l_3 \geq \dots$ . Moreover, if the values of  $l_x$  and  $m_x$  in Fig. 1 (Sandhu *et al.*, 2010) are used to calculate the net reproductive rate ( $R_0$ ), then values are significantly different than those given in Table 3 of Sandhu *et al.* (2010) are obtained. Shi *et al.* (2012) used the results of Sandhu *et al.* (2010) in their study. Because the errors in Sandhu *et al.* (2010) are obvious, researchers that used results of Sandhu *et al.* (2010) may need to re-evaluate their conclusions. (According to <http://www.bioone.org/doi/full/10.1603/EN10038>, the

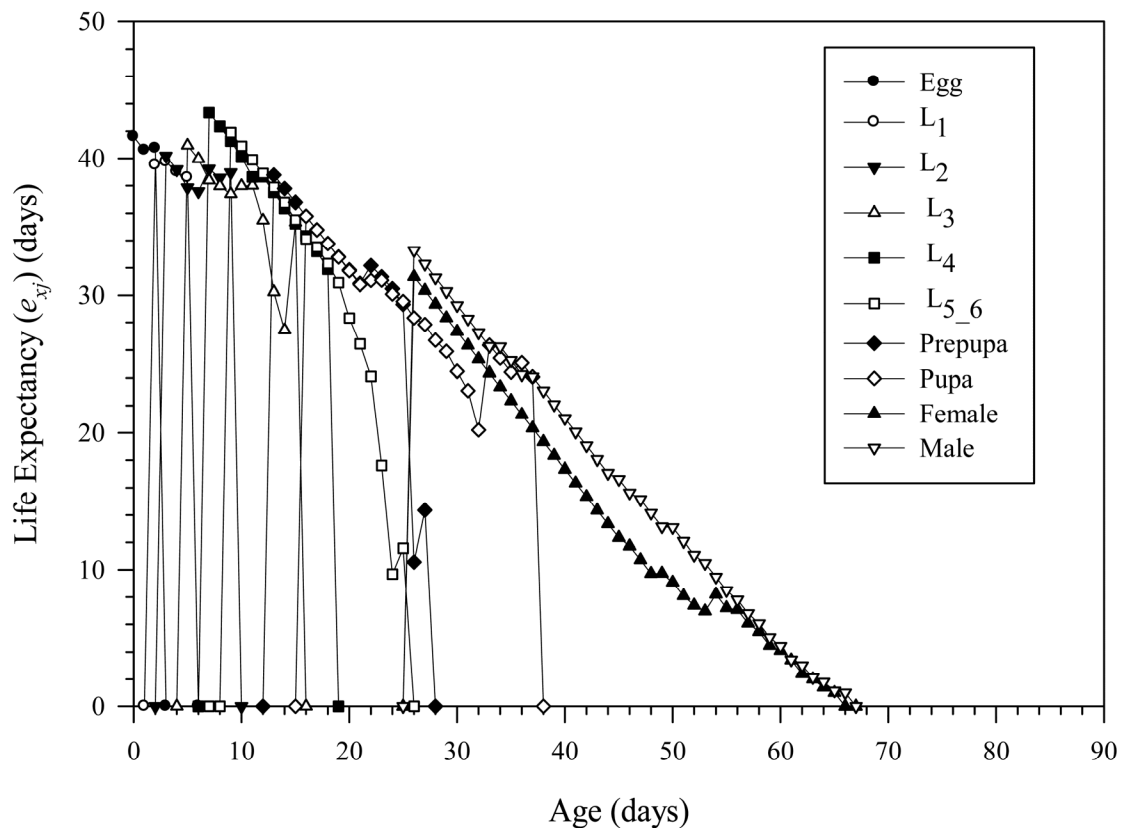


Fig. 4. Age-stage specific life expectancy ( $e_{xj}$ ) of *Helicoverpa armigera* reared at 29°C.

article of Sandhu et al. (2010) has been withdrawn at the request of the authors due to numerous errors that cannot readily be corrected by publishing an erratum.) Taking examples of *H. armigera* life tables, this problem can also be seen in Fig. 1 of Mironidis and Savopoulou-Soultani (2008) and in Fig. 1 of Liu et al. (2004). In the former, the authors constructed the age-specific survival rate ( $l_x$ ) based on a female age-specific life table, and, in the latter, the authors constructed the age-specific survival rate ( $l_x$ ) based on the stage-structured life table. Moreover, calculating fecundity ( $m_x$ ) based on the adult age, e.g., Fig. 3 of Mironidis and Savopoulou-Soultani (2008), results in a miscalculation of the fecundity curve. These

artificial manipulations and assumptions erroneously diminish the real variability among individuals, which consequently will result in errors in the survival and fecundity curves (Chi, 1988; Yu et al., 2005; Chi and Su, 2006; Huang and Chi, 2012a). To address the errors in life tables based on the adult age, Yu et al. (2005) and Chi and Su (2006) provided a detailed explanation and a mathematical proof.

The relationship between the net reproductive rate, the mean female fecundity, the number of emerged females, and the total number of individuals used in the life table study are consistent with the theoretical proof (Chi, 1988). As noted by Chi and Yang (2003), the estimated values from both the jackknife and the

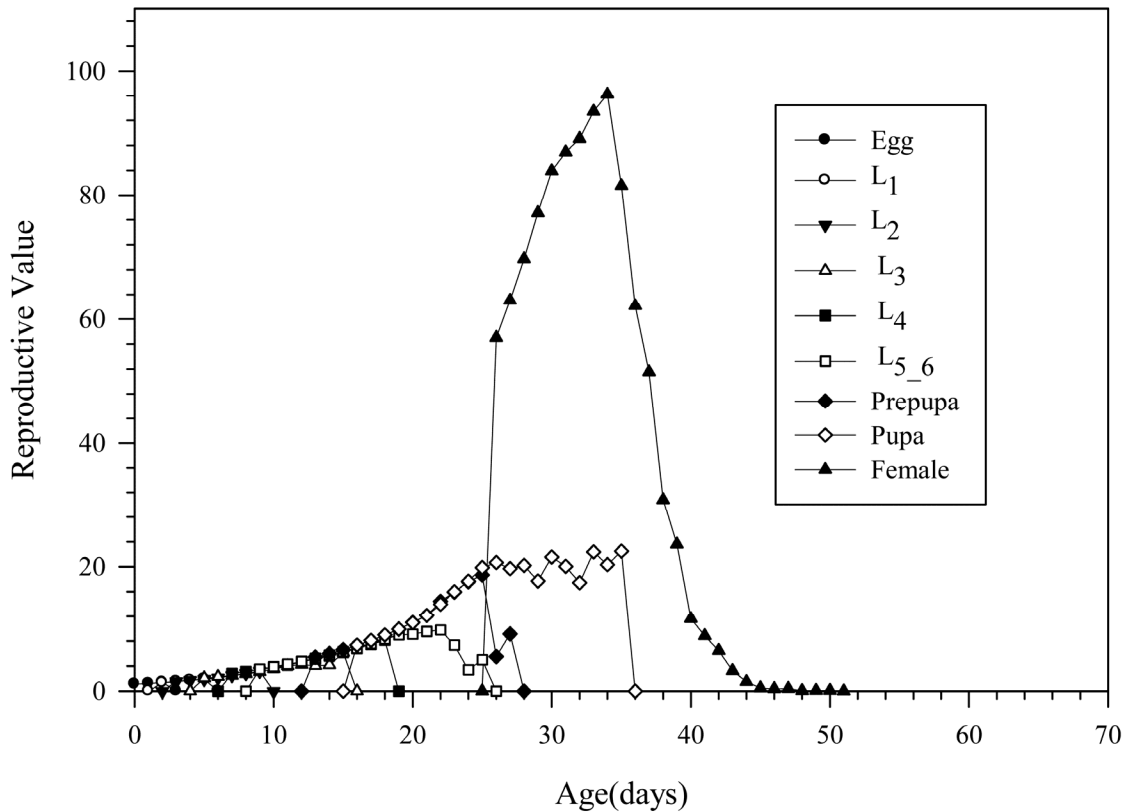


Fig. 5. Age-stage specific reproductive value ( $v_{xj}$ ) of *Helicoverpa armigera* reared at 29°C.

bootstrap methods showed slight inconsistencies. This question deserves further attention.

The results of this study showed that *H. armigera* reared at 29°C had a lighter pupal weight and poorer reproductive performance than the individuals reared at 25°C. These differences primarily resulted from a shorter pre-adult and oviposition duration. However, the pre-adult survival did not differ substantially. The larger gap between the curves of the total number of eggs and the number of hatched eggs in Fig. 1 indicates the poor hatchability of eggs at 29°C compared to those at 25°C (Fig. 1 of Jha *et al.*, 2012). These features were consequently expressed in by the very minor differences in  $r$  and  $\lambda$  between

rearing at 29°C and at 25°C and by the significantly lower  $R_0$  and  $GRR$  at 29°C (Table 2). Thus, per capita labor cost and rearing cost of *H. armigera* at 29°C may be higher due to a lower harvest.

The means and variance of the population parameters estimated by the jackknife and bootstrap resampling methods were also compared in this paper. The bootstrap method generated a normal distribution of estimated means, facilitating further robust statistical examination (Fig. 6). Efron (1982) reported that the bootstrap technique has a higher reliability than the jackknife technique for estimating variances. By using the bootstrap technique every bootstrap sample can be generated differently by

Table 2. Mean  $\pm$  S.E. of the population parameters of *Helicoverpa armigera* reared at 29°C using the jackknife and bootstrap methods

Population parameters	Jackknife		Bootstrap	
	29°C	25°C	29°C	25°C
	Mean $\pm$ S.E. <i>n</i> = 104	Mean $\pm$ S.E. <i>n</i> = 106	Mean $\pm$ S.E. <i>n</i> = 10,000	Mean $\pm$ S.E. <i>n</i> = 10,000
Intrinsic rate ( <i>r</i> ) (d <sup>-1</sup> )	0.1029 $\pm$ 0.011	0.1015 $\pm$ 0.007	0.0985 $\pm$ 0.0001 <sup>a</sup>	0.0993 $\pm$ 0.0001 <sup>a</sup>
Finite rate ( $\lambda$ ) (d <sup>-1</sup> )	1.1083 $\pm$ 0.0128	1.1068 $\pm$ 0.008	1.1040 $\pm$ 0.0001 <sup>a</sup>	1.1040 $\pm$ 0.0001 <sup>a</sup>
Net reproductive rate ( <i>R</i> <sub>0</sub> ) (offspring/individual)	40.2 $\pm$ 15.4 <sup>a</sup>	104.5 $\pm$ 32.8 <sup>a</sup>	40.2 $\pm$ 0.2	105 $\pm$ 0.3
Mean generation time ( <i>T</i> ) (d)	36.7 $\pm$ 0.9	46.3 $\pm$ 0.9	36.7 $\pm$ 0.01	46.4 $\pm$ 0.01
Gross reproduction rate ( <i>GRR</i> ) (offspring/individual)	68.6 $\pm$ 25.81 <sup>a</sup>	207.4 $\pm$ 62.6 <sup>a</sup>	68.1 $\pm$ 0.3	209.2 $\pm$ 0.7

Means of a population parameter of 29°C and 25°C under the Jackknife or Bootstrap followed by the same letter are not significantly different ( $p > 0.05$ ) using the U test.

sampling with replacement. In this way, bootstrapping creates variability in  $R_{0,B}$  and  $GRR_B$ . Even with the same number of replicates  $m$ , different  $R_{0,B}$  and  $GRR_B$  will be obtained. The variability depends on the size of  $m$ . The variability diminishes with the increasing  $m$ , but can always be observed in the variance and standard error as well as in the frequency distribution of  $R_{0,B}$  and  $GRR_B$ . Moreover, the  $p$ -value does not always decrease with the increase in bootstrap number  $m$  (Efron and Tibshirani, 1993). On the other hand, there is always exactly one jackknife result, and all the frequency distributions from the jackknife technique in Fig. 6 will be the same.

In the case of the jackknife technique the  $R_{0,J}$  will be zero if the omitted individual is a male or one that died in the pre-adult stage. This effect can be observed in the figure that shows the jackknife results (Fig. 6). A net reproductive rate of zero means that the population does not produce any offspring, and in that case we cannot calculate the intrinsic rate. However, the intrinsic rate of increase can be calculated by omitting one male individual or one that died before the adult stage. This outcome contradicts the life table theory. We therefore conclude that the

jackknife technique should not be used for estimating the standard error of the net reproductive rate. Moreover, the application of the jackknife technique to  $R_0$  was mathematically invalidated by Huang and Chi (2012b), and they also suggested not to use it for the estimation of the variability of  $R_0$ . Therefore, the mathematical validation of the choice of resampling techniques for other parameters requires further study.

In this paper, the Euler-Lotka equation (Eq. 1) was used to calculate the intrinsic rate of increase instead of the approximation method ( $T = \sum x l_x m_x / \sum l_x m_x$ ) suggested by Birch (1948). David (1995) and Case (2000) pointed out the issues of variation in the Euler-Lotka formula with the age index from zero and one. If the age is indexed from 1 ( $l_1=1$ ), Goodman (1982) suggested that the Euler-Lotka equation is

$$\sum_{x=1}^{\infty} e^{-rx} l_x m_x = 1 \quad 13$$

Both Eq. 1 and Eq. 13 give the same result for the age index from zero and 1, respectively. The following calculations based on a hypothetical cohort (Fig. 7)

Table 3. Population projection of the hypothetical cohort and growth rate

Time ( <i>t</i> )	Age ( <i>x</i> )				Total	Growth rate ( $\lambda$ )
	0	1	2	3		
0	10.00	0.00	0.00	0.00	10.00	0.5000
1	0.00	5.00	0.00	0.00	5.00	2.0000
2	5.00	0.00	5.00	0.00	10.00	1.5000
3	10.00	2.50	0.00	2.50	15.00	0.8333
4	5.00	5.00	2.50	0.00	12.50	1.5000
5	10.00	2.50	5.00	1.25	18.75	1.2667
6	13.75	5.00	2.50	2.50	23.75	1.0789
7	12.50	6.88	5.00	1.25	25.63	1.3171
8	18.13	6.25	6.88	2.50	33.75	1.2222
9	22.50	9.06	6.25	3.44	41.25	1.1742
10	25.00	11.25	9.06	3.13	48.44	1.2548
11	32.50	12.50	11.25	4.53	60.78	1.2159
12	39.53	16.25	12.50	5.63	73.91	1.2061
13	46.88	19.77	16.25	6.25	89.14	1.2323
14	58.52	23.44	19.77	8.13	109.84	1.2169
15	71.09	29.26	23.44	9.88	133.67	1.2160
16	86.02	35.55	29.26	11.72	162.54	1.2241
17	105.78	43.01	35.55	14.63	198.96	1.2183
18	128.73	52.89	43.01	17.77	242.40	1.2188
19	156.68	64.37	52.89	21.50	295.44	1.2212
20	191.65	78.34	64.37	26.45	360.80	1.2191

help to better understand the issue. In Fig. 7,  $f_x (= m_x)$  is the age specific fecundity, i.e., the total number of female offspring produced by a female during the age interval  $x \leq \text{age} < x + 1$ . The age-specific survival rate ( $s_x$ ) is the probability of an individual of age  $x$  surviving to  $x+1$ . The age-specific survival rate can also be defined as  $l_x$ , i.e., the survival rate from birth to age  $x$ . Arranging the data of Fig. 7 in a Lewis-Leslie Matrix, we get the following matrix

$$M_0 = \begin{bmatrix} f_0 & f_1 & f_2 & f_3 \\ s_0 & 0 & 0 & 0 \\ 0 & s_1 & 0 & 0 \\ 0 & 0 & s_2 & 0 \end{bmatrix} = \begin{bmatrix} 0 & 1 & 2 & 1 \\ 0.5 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 0.5 & 0 \end{bmatrix}$$

In this matrix, age is indexed from zero. To find the eigenvalues of matrix  $M_0$ ,

we solve the characteristics equation  $|M - \lambda I| = 0$  (where  $I$  is the identity matrix) as

$$\lambda^4 - 0.5\lambda^2 - \lambda - 0.25 = 0 \tag{14}$$

Solving Eq. 14 by iterative bisection method, we obtain the dominant eigenvalue,  $\lambda = 1.21978$ , which is the finite rate of increase at a stable age distribution. The population projection given in Table 3, based on this hypothetical data also shows the  $\lambda$  of this cohort approaching to 1.21978 as time ( $t$ ) increases. The  $\lambda$  in Table 3 is the growth rate of the population from  $t$  to  $t+1$ .

If for this cohort we use the Euler-Lotka equation as in Eq. 1, i.e.,  $\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1$ , we get the function:  $0.5e^{-2r} + e^{-3r} + 0.25e^{-4r} = 1$ , where  $l_0 = 1$ ,  $l_1 = s_0 = 0.5$ ,  $l_2 = s_0 s_1 = 0.5$ ,  $l_3 = s_0 s_1 s_2 =$

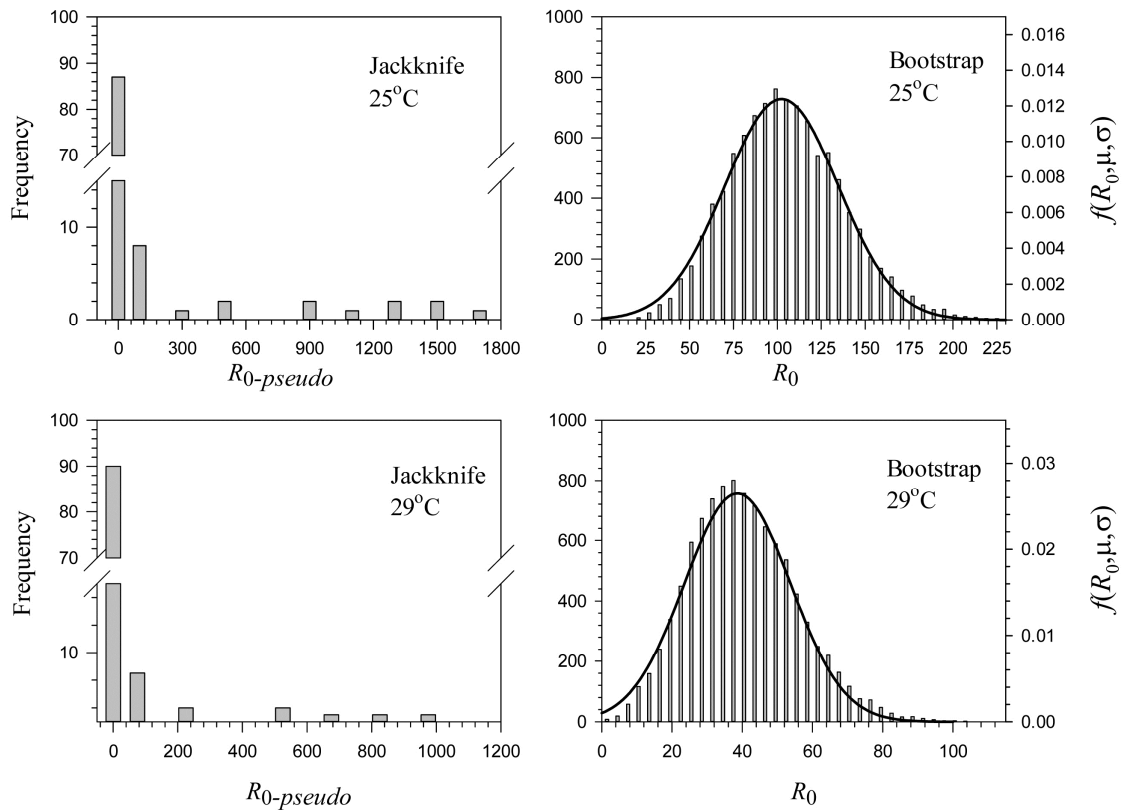


Fig. 6. Frequency distribution of pseudo-values estimated by the jackknife technique and sample means estimated by using the bootstrap technique (10,000 bootstraps) of the net reproductive rate of *Helicoverpa armigera* reared at 25°C and 29°C.

0.25. By solving this function by iterative bisection method, we get  $r = 0.19867$  ( $\lambda = e^r = 1.21978$ ) which is the same value obtained from Eq. 14. If we use the Euler-Lotka equation with age indexed from zero ( $l_0 = 1$ ), as (e.g., Meyer *et al.*, 1986; Maia *et al.*, 2000)

$$\sum_{x=0}^{\infty} e^{-rx} l_x m_x = 1 \quad 15$$

we get the function:  $0.5e^{-r} + e^{-2r} + 0.25e^{-3r} = 1$ . By solving this function, we get  $r = 0.31191$  ( $\lambda = e^r = 1.36603$ ) which is inconsistent with the projection results and the eigenvalue

analysis of  $M_0$ .

Furthermore, arranging the data of Fig. 8 in a Lewis-Leslie Matrix, we get the matrix

$$M_1 = \begin{bmatrix} f_1 & f_2 & f_3 & f_4 \\ s_1 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 \\ 0 & 0 & s_3 & 0 \end{bmatrix} = \begin{bmatrix} 0 & 1 & 2 & 1 \\ 0.5 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 0.5 & 0 \end{bmatrix}$$

In this matrix, age is indexed from 1 ( $l_1 = 1$ ). To find the eigenvalue of matrix  $M_1$ , we get the same characteristics equation as Eq. 14:  $\lambda^4 - 0.5\lambda^2 - \lambda - 0.25 = 0$ . Thus, we will certainly obtain the same finite rate  $\lambda = 1.21978$  as  $M_0$ .

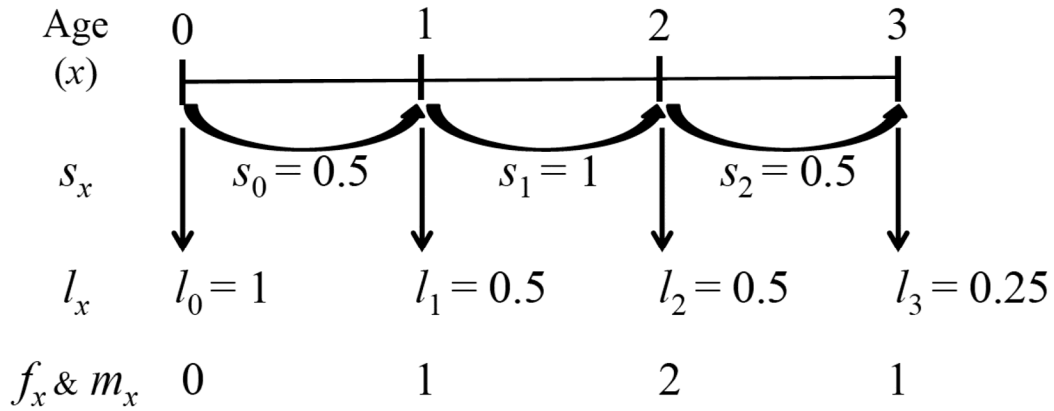


Fig. 7. The age notations, the age-specific survival rate ( $s_x$  and  $l_x$ ) and the age-specific fecundity ( $f_x$  and  $m_x$ ) of a hypothetical cohort with age indexed from 0.

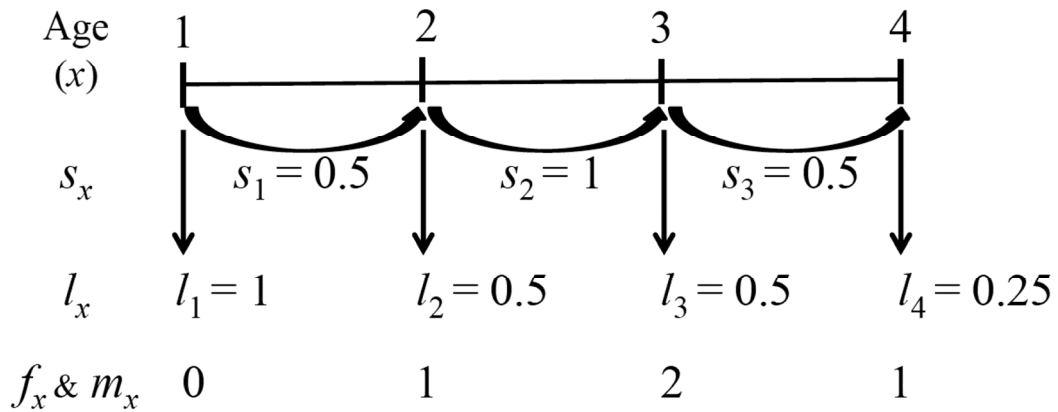


Fig. 8. The age notations, the age-specific survival rate ( $s_x$  and  $l_x$ ) and the age-specific fecundity ( $f_x$  and  $m_x$ ) of a hypothetical cohort with age indexed from 1.

If we use the Euler-Lotka equation with age indexed from one as

$$\sum_{x=1}^{\infty} e^{-r(x+1)} l_x m_x = 1 \quad 16$$

we get the function:

$$0.5e^{-3r} + e^{-4r} + 0.25e^{-5r} = 1 \quad \text{where } l_1=1, l_2=s_1=0.5, l_3= s_1 s_2= 0.5, l_4= s_1 s_2 s_3=$$

0.25. By solving this function, we get  $r = 0.14621$  ( $\lambda = 1.15744$ ) which is also incorrect. However, if we use the Euler-Lotka equation as in Eq. 13, i.e.  $\sum_{x=1}^{\infty} e^{-rx} l_x m_x = 1$ , we get the same function that we get from using Eq. 1:  $0.5e^{-2r} + e^{-3r} + 0.25e^{-4r} = 1$ , and the same intrinsic rate of increase ( $r = 0.19867$ ) and finite rate ( $\lambda = e^r = 1.21978$ ).



Thus, in order to apply the Euler-Lotka equation correctly when estimating the intrinsic rate of increase  $r$ , it is important to choose the right form as mentioned above, based on the formation of  $l_x$  and  $m_x$  in this study.

A laboratory life table is a key to estimate the intrinsic rate of increase under a given set of conditions (Gutierrez, 1996). The intrinsic rate of increase is the appropriate life table parameter and a good bioclimatic index for comparing the fitness of populations across diverse climatic and food-related conditions (Messenger, 1964; Southwood, 1966; Smith, 1991; Kingsolver and Huey, 2008). Characterizing the demography of an insect under varying conditions is an essential task for understanding pests in natural environments. In this regard, the age-stage, two-sex life tables provide a comprehensive description of the demography of *H. armigera* under a given set of conditions. Based on this age-stage, two-sex life table analysis, it can be concluded that rearing *H. armigera* at 29°C is less conducive to maintaining a colony in a laboratory than rearing them at 25°C.

## Acknowledgments

We thank Prof. Dr. S. J. Tuan and Dr. C. F. Lai for their support in this study. This project is financially supported by NSC 98-2313-B-005-020-MY3 and 99AS-5.3.1-ST-aG.

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**Received: June 5, 2012**

**Accepted: June 18, 2012**

# 利用玉米穗蟲 *Helicoverpa armigera* (Hübner) 的生命表與 Jackknife 和 Bootstrap 方法之討論與 Euler-Lotka Equation 的變異

陳 樂<sup>1,2</sup>、齊 心<sup>1</sup>、唐立正<sup>1\*</sup>

<sup>1</sup> 國立中興大學昆蟲學系 40227 台中市國光路 250 號

<sup>2</sup> Plant Protection Directorate, Department of Agriculture, Hariharbhawan, Lalitpur, Nepal

## 摘 要

本研究以年齡齡期兩性生命表理論分析玉米穗蟲 *Helicoverpa armigera* (Hübner) 在實驗室 29°C 的環境條件下取食人工飼料之生命表。以孵化卵數計算年齡別繁殖率可正確呈現不同日齡雌蟲所產的卵之孵化率的變化，並準確的呈現玉米穗蟲的生物學特性。玉米穗蟲的內在增殖率 ( $r$ )、終極增殖率 ( $\lambda$ )、平均世代時間 ( $T$ )、淨增殖率 ( $R_0$ ) 以及粗繁殖率 ( $GRR$ ) 分別為  $0.1029 \text{ d}^{-1}$ 、 $1.1083 \text{ d}^{-1}$ 、 $36.7 \text{ d}$ 、 $40.2 \text{ offspring}$  以及  $68.6 \text{ offspring}$ ；淨增殖率及雌蟲平均繁殖力間的關係與理論證明相符。本研究指出，以人工飼料飼養玉米穗蟲的方式在 29°C 的環境條件並不如 25°C 下有利。利用 jackknife 和 bootstrap 兩種方法估計生命表族群參數的變方與標準誤差，以 jackknife 重新取樣的方法所得到的 pseudo values 之頻率分布在常態檢定下是失敗的，但 bootstrap 的結果符合常態分布檢定。因為在使用 jackknife 方法時會產生沒有生物學意義的淨增殖率為零的 pseudo values，因此 jackknife 的方式不應該用來估算淨增殖率的標準誤差。jackknife 應用在其他族群參數的估算上需要有更進一步的探討。為了正確估算內在增殖率，Euler-Lotka 方程式中的年齡標示必須符合存活率和繁殖率所定義的年齡標示。由於年齡齡期兩性生命表準確描述昆蟲的存活、發育、齡期分化以及繁殖，我們建議昆蟲的生命表分析應使用兩性生命表。

**關鍵詞：**人口統計學、內在增殖率、Euler-Lotka 方程式、Jackknife、Bootstrap。

\*論文聯繫人

Corresponding email: lctang@dragon.nchu.edu.tw

Life Table of *Helicoverpa armigera* 375